

A TAXONOMIC STUDY OF THE GALÁPAGOS ENDEMIC VARRONIA (CORDIACEAE) SPECIES WITH NOMENCLATURAL NOTES

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ABSTRACT

This study revises the taxonomy of *Varronia* P. Br. (Cordiaceae) species endemic to the Galapagos Islands and presents a key that can more reliably distinguish the species using vegetative characters alone. We conclude that there are four endemic species of Galapagos *Varronia* distributed across ten islands: *V. canescens* Andersson (syn = *V. anderssonii*, nom. illeg.), *V. leucophlyctis* (Hook. f.) Andersson, *V. scouleri* (Hook. f.) Andersson, and *V. revoluta* (Hook. f.) Andersson. Although most species share island distributions, species are not found in close proximity together and no obviously intermediate or putatively hybrid individuals were observed. The endemic species appear to be distylous, and preliminary data suggest these species may be obligate outcrossers. The findings of our study will assist efforts by park managers and other researchers to determine the conservation status of each species and to develop appropriate conservation measures in line with the life-history of the species.

RESUMEN

El propósito de este estudio fue revisar la taxonomía de las especies endémicas de *Varronia* P. Br. (Cordiaceae), de las Islas Galápagos y hacer una clave taxonómica que pueda distinguir con mayor fiabilidad las especies usando solo caracteres vegetativos. Llegamos a la conclusión que hay cuatro especies endémicas de *Varronia* en Galápagos, distribuidas en diez islas: *V. canescens* Andersson (syn = *V. anderssonii*, nom. illeg.), *V. leucophlyctis* (Hook. f.) Andersson, *V. scouleri* (Hook. f.) Andersson, y *V. revoluta* (Hook. f.). Aunque la mayoría de especies compartan su distribución en las islas, las especies no se encuentran muy cerca entre sí y obviamente no fueron observados individuos intermedios o supuestamente híbridos. Las especies endémicas parecen ser de doble estilo¹ distilas, y los datos preliminares indican que estas especies pueden ser alógamas obligadas. Los hallazgos de nuestros estudios ayudarán a los encargados de gestionar el Parque Nacional y a otros investigadores para determinar el estatus de conservación de cada especie y desarrollar medidas adecuadas de conservación de acuerdo con la historia vital de las especies.

INTRODUCTION

Background

Within the past several decades, the Galápagos Islands have become increasingly exposed to threats from invasive species and rapidly expanding human populations (Atkinson et al. 2010; Tapia et al. 2010). Invasive nonnative species pose the greatest threat to the native and endemic species on the Islands (Trueman et al. 2010), and the Galápagos are particularly vulnerable to invasion by alien species (Denslow et al. 2009; Reaser et al. 2007). Accurate identification and documentation of the flora of the Galápagos is essential for conservation efforts, particularly for those species that suffer from taxonomic uncertainty. The purpose of this study was to review and update the characterization of the endemic species of genus *Varronia* and to create a more complete identification key for them based on foliar morphology. Scientists have been unable to accurately evaluate these species for conservation status because morphological distinctions between species do not hold up in practice. This uncertainty may have discouraged research on these species of *Varronia*.

Site Description

The Galápagos archipelago is composed of volcanic islands located in the Pacific Ocean with a total land area of 7880 km² within a geographical area of 45,000 km² (Neill & Trewick 2008). The archipelago is approximately 1000 kilometers west of Ecuador and is the product of a stationary mantle hotspot (Morgan 1971); the

¹Las plantas heterostilas que tiene dos formas de flores son definidas de doble estilo (Heterostylous plants having two flower morphs are termed distylous).

archipelago has never been in contact with any continental land mass. The ages of the individual islands increase eastward due to the movement of the Nazca plate on which the Galápagos are located (Rassmann 1997). From the velocity of the plate motion, scientists estimate that none of the islands above ocean level is older than five million years, and radiometric data predict a more recent origin of the present archipelago (White et al. 1993). The older islands are estimated to be between three and four million years old, while the younger islands may be one to two million years old (Hickman & Lipps 1985). The flora and fauna that dispersed to the Galápagos originated in various regions around the Pacific basin, including North, Central, and South America, the Caribbean, and Asia/Australasia (Grehan 2001; Jackson 1993). The climate of the Galápagos is extremely arid compared to most tropical archipelagos. The Islands experience a warm season from January to May, during which time lowland vegetation reaches its peak, and a cool season from June to December, where lowlands remain dry while highlands remain constantly wet from a mixture of light rain and mist (McMullen 1999).

Today, the Islands have a well-documented flora of 614 indigenous angiosperm species, of which 238 are endemic, 314 are native and 62 putatively so. The Islands also host 825 introduced species of which 324 are considered to be naturalized (McMullen 2011). The Galápagos Islands consist of three ecological zones that include the Littoral (Coastal) Zone, the Arid Lowlands, and the Moist Uplands (Johnson & Raven 1973). The Littoral Zone occupies the shoreline and is comprised of salt-tolerant vegetative species; the Arid Lowlands are characterized by *Opuntia* cacti and shrubby, herbaceous species that tolerate dry living conditions much of the year; the Moist Uplands are characterized by ferns, sedges, and evergreen tree species, including *Scalesia* (McMullen 1999). *Varronia* species from this study are primarily found in the Arid Lowlands, but may occasionally be found in the Moist Uplands.

Taxonomy and Phylogenetic History of Galapagos *Varronia* species

The angiosperm family Cordiaceae is represented in the archipelago by two genera, *Cordia* L. and *Varronia* P. Br., and seven species: *C. lutea* Lam., *C. alliodora* (Ruiz & Pav.) Oken, *V. polycephala* Lam., *V. canescens* Anderss., *V. leucophlyctis* (Hook. f.) Anderss., *V. revoluta* (Hook. f.) Anderss., and *V. scouleri* (Hook. f.) Anderss. (Jaramillo Díaz & Guézou 2011; Wiggins & Porter 1971). Of these seven, four are endemic (*V. canescens*, *V. leucophlyctis*, *V. revoluta*, and *V. scouleri*), with the remainder either native (*V. polycephala*) or introduced (*C. lutea*, *C. alliodora*). Until recently, all species were placed in the genus *Cordia*, but Miller and Gottschling (2007) resurrected the genus *Varronia* to circumscribe the monophyletic group of shrubby species limited to the Americas. *Varronia* species are multi-stemmed shrubs with regularly serrate leaf margins and have inflorescences that are condensed, capitate, spicate, or if cymose, then small and few-flowered; their pollen grains are porate. By contrast, *Cordia* species are single or few-stemmed trees with leaf margins that are entire or irregularly sharply dentate on the apical half and have inflorescences that are cymose; their pollen grains are colpate.

Varronia is an entirely New World genus with approximately 100 species ranging from Arizona to Argentina, with the predominance of the species being limited to the frost-free sub-tropics (Miller and Gottschling 2007). The presence of *Varronia* in the Galápagos is likely due to long-distance seed dispersal by frugivorous birds (McMullen 2009; Itow 2003) from western South America. Porter (1983) hypothesized that three of the endemic species of the “*leucophlyctis*-complex” (*V. canescens*, *V. leucophlyctis*, and *V. scouleri*) are most closely related to *V. macrocephala* Desv. (syn.= *V. polyantha* Benth.), a native of Columbia and Peru, and the findings of Weeks et al. (2010) are consistent with this hypothesis.

Of the four endemic species, *V. revoluta* is the most easily distinguished based on its linear, revolute leaves and tubular corolla. The three remaining endemic species are morphologically similar; these members of the so-called “*leucophlyctis*-complex” are quite difficult to distinguish reliably. The taxonomic key produced by Wiggins and Porter (1971) provides diagnoses based on leaf and calyx pubescence:

Leaves lanceolate, margins not revolute; corolla funnelform, the tube less than twice as long as width of limb; upper surface of leaves with erect or ascending hairs, not appressed-pubescent.

Upper surface of leaves with both simple and stout, forked, or stellate and simple hairs with conspicuously pustulate bases; calyx lobes clothed with coarse simple and forked hairs much longer than those on lower part of cup _____ *V. canescens*

Upper surface of leaves bearing only simple, erect or slightly curved, usually more slender hairs; calyx lobes with same-sized hairs as base of cup.

Stems and lower surface of leaves only stiff, erect, and simple hairs _____	<i>V. leucophlyctis</i>
Stems and lower surface of leaves bearing scattered, erect, simple hairs and a close cover of minute, appressed, stellate hairs _____	<i>V. scouleri</i>

In practice, however, their diagnoses do not cover the full range of *Varronia* species variation and do not provide the necessary separation needed for accurate and reliable identification.

Molecular phylogenetic data have not been able to fully resolve questions regarding the origin and evolution of the endemic *Varronia* species. Sequence data from the nuclear and chloroplast genomes indicate a possibly reticulate evolutionary history for the endemic species, with nuclear ribosomal DNA internal transcribed spacer (ITS) data supporting separate origins of *V. revoluta* and the species of the leucophlyctis-complex and chloroplast *ndhF* genic data supporting a single radiation event. Moreover, sequence data were not able to distinguish separate lineages within the complex. Fossil-based calibrations of the phylogeny indicate lineages are younger than some of the extant islands in the archipelago (< 4.5 Mya) and that the complex is likely less than 2 Mya. This finding suggests species boundaries may be difficult to distinguish because of the relative youth of this species complex (Weeks et al. 2010).

Rationale

The difficulty in distinguishing these endemic species may have conservation implications. Currently, the one endemic species easily identifiable, *V. revoluta*, is considered “Near Threatened” by the International Union for the Conservation of Nature (IUCN), whereas *V. scouleri* is considered “Vulnerable” (Tye 2000c,d). A Vulnerable species is one that has been categorized by the IUCN as likely to become endangered unless the circumstances threatening its survival and reproduction improve. A status of Near Threatened is assigned to a species that may be considered threatened with extinction in the near future, although it does not currently qualify for the Threatened status. Both *V. canescens* and *V. leucophlyctis* are classified as “Data Deficient” due to taxonomic uncertainty (Tye 2000a,b). Data Deficient is a category applied to a species when the available information, including abundance and distribution, is not sufficient for a proper assessment of conservation status to be made. Introduced species have become increasingly represented in the flora and fauna of the Galápagos Islands (Atkinson et al. 2010). The effects of these introduced species on the indigenous plants and animals of the archipelago must be monitored because so many of the species (39%) are endemic, such as the *Varronia* in this study (McMullen 2011). Because of the relatively unknown impact of introduced species on many endemic species, it is important to establish and maintain an accurately documented floral baseline for reference in future studies. Documentation of this sort, which includes updated nomenclature, taxonomic keys, and distribution maps, will provide useful information to Galápagos researchers, park personnel, and visiting researchers as they strive to develop sensible and effective conservation programs.

Objectives

The major objectives of this study were: 1) revise the nomenclature of the *Varronia* Galápagos endemics, 2) revise the leaf, trichome, and calyx lobe morphological descriptions for each *Varronia* species, and 3) produce a more reliable key for the endemic *Varronia* using characters that can be used in the field.

MATERIALS AND METHODS

A total of 348 herbarium specimens were examined: 133 specimens collected by CKM during trips to the Galápagos in 2005 and 2007 (JMUH) and an additional 215 loaned specimens collected between the years 1825 and 1983. A total of three specimens were obtained from the Brooklyn Botanic Garden (BKL), 49 from the California Academy of Sciences (CAS), eight from the New York Botanical Garden (NY), 56 from Harvard University (GH), 26 from the University of Copenhagen (C), 55 from the Swedish Museum of Natural History (S), and 18 from the Royal Botanic Gardens at Kew (K). Eight type specimens from K and one type specimen from S, as well as photographs of three type specimens from the University of Cambridge Herbarium (CGE) were studied for a total of 11 type specimens included in this study. A total of 81 specimens of *Varronia canescens*, 95 specimens of *V. leucophlyctis*, 89 specimens of *V. scouleri*, and 83 specimens of *V. revoluta* were examined.

Specimens were first sorted into piles based on relative similarities in leaf shape, regardless of the identification on the label. The specimens were then examined with a dissecting microscope and the piles were readjusted based on both leaf shape and morphological similarities in leaf pubescence. During this process, four distinct sets of morphological leaf shape and leaf pubescence characteristics were observed, as described in the following species narratives. In addition, measurements of leaf length and width on two leaves per specimen were taken, and observations of calyx length and pubescence were also observed. This information is also included in the species descriptions.

Endocarp structure of fruits from 17 different individuals was observed. Only JMUH specimens were utilized. Few specimens from other herbaria had fruits available, and most of these specimens were considerably older and in more fragile condition. Preparation of the endocarp included boiling fruits in distilled water for 15 minutes, and soaking them in a room temperature water bath for a 24-hour period to help loosen the fleshy material surrounding the endocarp. Any remaining material was removed with tweezers before observing the endocarp under a dissecting scope. Endocarp structure varied minimally between individuals observed, and was not useful in distinguishing species. This information is therefore not included in the new keys.

To obtain detailed images of the plants' leaf surface morphologies, a LEO 1340 VP Scanning Electron Microscope was used at the James Madison University SEM/EDS Regional Facility. The SEM operated with an acceleration voltage of 25 kV, a spot size of 300 (equivalent to a probe current of 102 picoamps), and a working distance of 25 mm. Samples of dried herbarium material were coated with gold from a sputter coater prior to imaging, and the images obtained are secondary electron images. The specimens selected to obtain SEM images were chosen as representative samples of the species based on observations with a dissecting microscope. In addition to work at James Madison University, a trip to the Galápagos Islands in February 2011 allowed direct observation of live specimens in the field, observation of herbarium specimens at the Charles Darwin Research Station (CDS), and field testing of the new taxonomic keys (Tables 1 and 2).

MORPHOLOGICAL CHARACTERIZATIONS

In the following species characterizations, all descriptions of leaf shape and size, leaf pubescence and color, and calyx pubescence and size at anthesis are the result of this morphological study. All other descriptions are from Wiggins and Porter (1971), and are cited as such within each description.

1. *Varronia revoluta* (Hook. f.) Andersson, Kongl. Vetensk.-Akad. Handl. 1853:204. 1855. = *Cordia revoluta* Hook. f., Trans. Linn. Soc. London 20:199. 1847. TYPE: ECUADOR. GALÁPAGOS ISLANDS. Charles Island (Florea Island): Sep 1835, Charles Darwin s.n. (HOLOTYPE: CGE 00287). = *Lithocardium revolutum* (Hook. f.) Kuntze, Revis. Gen. Pl. 2:977. 1891. = *Sebestena revoluta* (Hook. f.) Friesen, Bull. Soc. Bot. Genève 2(24):183. 1933, nom. illeg. = *Varronia revoluta* (Hook. f.) Borhidi, Acta Bot. Hung. 34:383. 1988, nom. illeg.

= *Cordia revoluta* Hook. f. var. *nigricans* Hook. f., Trans. Linn. Soc. London 20:199. 1847. TYPE: ECUADOR. GALÁPAGOS ISLANDS. Albemarle Island (Isabela Island): 1825, Macrae s.n. (LECTOTYPE, designated by Porter 1980: K 449166!; ISOLECTOTYPE: K 449167!).

= *Cordia linearis* Hook. f., Trans. Linn. Soc. London 20:199. 1847, nom. illeg. TYPE: ECUADOR. GALÁPAGOS ISLANDS. James Island (Santiago Island): 1835, Charles Darwin s.n. (LECTOTYPE, designated by Porter 1980: CGE 00286; ISOLECTOTYPES: K 449161!, K 449162!). = *Varronia linearis* (Hook. f.) Andersson, Kongl. Vetensk.-Akad. Handl. 1853:204. 1855. = *Sebestena linearis* (Hook. f.) Friesen, Bull. Soc. Bot. Genève 2(24):182. 1933. = *Lithocardium hookerianum* Kuntze, Revis. Gen. Pl. 2:976. 1891. = *Cordia hookeriana* (Kuntze) Gürke, Nat. Pflanzenfam. 4(3):83. 1893.

Species description.—*Varronia revoluta* is a slenderly branched shrub 2–4 m in height, with dark gray-brown, shallowly fissured bark marked by transversely elliptic lenticels; young twigs densely fine-pubescent with appressed simple hairs (Wiggins & Porter 1971). Leaves linear with strongly revolute margins, 2.5–11.0 cm long, 0.2–1.0 cm wide; adaxial surfaces dark green and densely pubescent, hairs white, simple, and appressed (Fig. 1a); abaxial surfaces lighter green and densely villous pubescent, with more robust appressed hairs found on the veins; midrib is markedly elevated (Fig. 2a). Inflorescence globose-capitate on a slender, terminal peduncle 1.0–5.0 cm long with appressed-pubescence (Wiggins & Porter 1971). Calyx broadly cup-shaped to nearly globose, 2.5–3.5 mm long, about 3.0 mm wide, slightly contracted at apex, shallowly 5-lobed, only slightly

TABLE 1. A comparison of the diagnostic traits among the four species of endemic *Varronia* in the Galápagos Islands.

	<i>V. revoluta</i>	<i>V. leucophlyctis</i>	<i>V. canescens</i>	<i>V. scouleri</i>
leaf shape	linear	broadly lanceolate	lanceolate	lanceolate
leaf margins	revolute	finely serrate to crenate	finely serrate to crenate	coarsely serrate
adaxial leaf surface	hairs white and all simple appressed; densely pubescent	hairs mostly clear, erect and simple	hairs clear or white, typically appressed or sometimes weakly erect, stellate and forked, sometimes simple; hairs almost completely absent on some leaves	hairs mostly clear or white, erect simple, forked, sometimes stellate
abaxial leaf surface	hairs simple; densely villous pubescent; more robust, appressed white hairs on veins	hairs mostly simple and erect; often densely pubescent; simple, robust hairs common on veins; hairs generally clear or faintly white	hairs appressed stellate, forked, and simple; densely; pubescent hairs clear or white	hairs appressed stellate and forked, sometimes simple; sparsely pubescent; noticeably more robust hairs on veins; hairs generally clear or faintly white
calyx hairs	hairs simple; densely villous, uniform length throughout	hairs erect and simple; noticeably longer on calyx lobes than on calyx tube	hairs appressed stellate, forked, and simple, uniform length throughout	hairs erect and simple, sometimes forked or stellate; simple hairs noticeably longer on calyx lobes than on calyx tube
calyx lobes	much shorter than calyx tube at anthesis	about as long as calyx tube at anthesis	as long as or shorter than calyx tube at anthesis	usually longer than calyx tube at anthesis

TABLE 2. A dichotomous key to the four species of endemic *Varronia* in the Galápagos Islands.

1. Leaves linear.
 2. Leaf margins revolute; adaxial leaf hairs white and all simple appressed, densely pubescent; abaxial leaf hairs simple, densely villous pubescent, with more robust, appressed white hairs on veins; calyx hairs simple, densely villous, and uniform length throughout; calyx lobes much shorter than calyx tube at anthesis _____ ***V. revoluta***
1. Leaves lanceolate.
 3. Adaxial leaf hairs almost entirely erect and simple; abaxial leaf hairs mostly simple and erect, with robust, simple hairs found on veins.
 4. Leaf margins finely serrate to crenate; calyx hairs erect and simple, noticeably longer on calyx lobes than on calyx tube; calyx lobes about as long as calyx tube at anthesis _____ ***V. leucophlyctis***
 3. Adaxial leaf hairs simple, forked, or stellate; abaxial leaf hairs simple, forked, or stellate.
 5. Leaf margins finely serrate to crenate; adaxial leaf hairs typically appressed or sometimes weakly erect, stellate and forked, sometimes simple; adaxial leaf hairs almost completely absent on some leaves; abaxial leaf hairs appressed stellate, forked, and simple, densely pubescent; calyx hairs appressed stellate, forked, and simple, uniform length throughout; calyx lobes as long as or shorter than calyx tube at anthesis _____ ***V. canescens***
 5. Leaf margins generally coarsely serrate; adaxial leaf hairs erect simple, forked, sometimes stellate; abaxial leaf hairs appressed stellate and forked, sometimes simple, sparsely pubescent, with noticeably more robust hairs on veins; calyx hairs erect and simple, sometimes forked or stellate, with simple hairs noticeably longer on calyx lobes than on calyx tube; calyx lobes usually longer than calyx tube at anthesis _____ ***V. scouleri***

turned outward in flower (Wiggins & Porter 1971); densely villous pubescent with simple hairs, uniform length throughout (Fig. 3a); calyx lobes much shorter than calyx tube at anthesis (Fig. 3a). Corolla white, usually 5-lobed (rarely 4), tubular, 7.0–12.0 mm long, 2.0–2.5 mm wide, with throat slightly narrowed, and lobes ascending-spreading to rotate (Wiggins & Porter 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

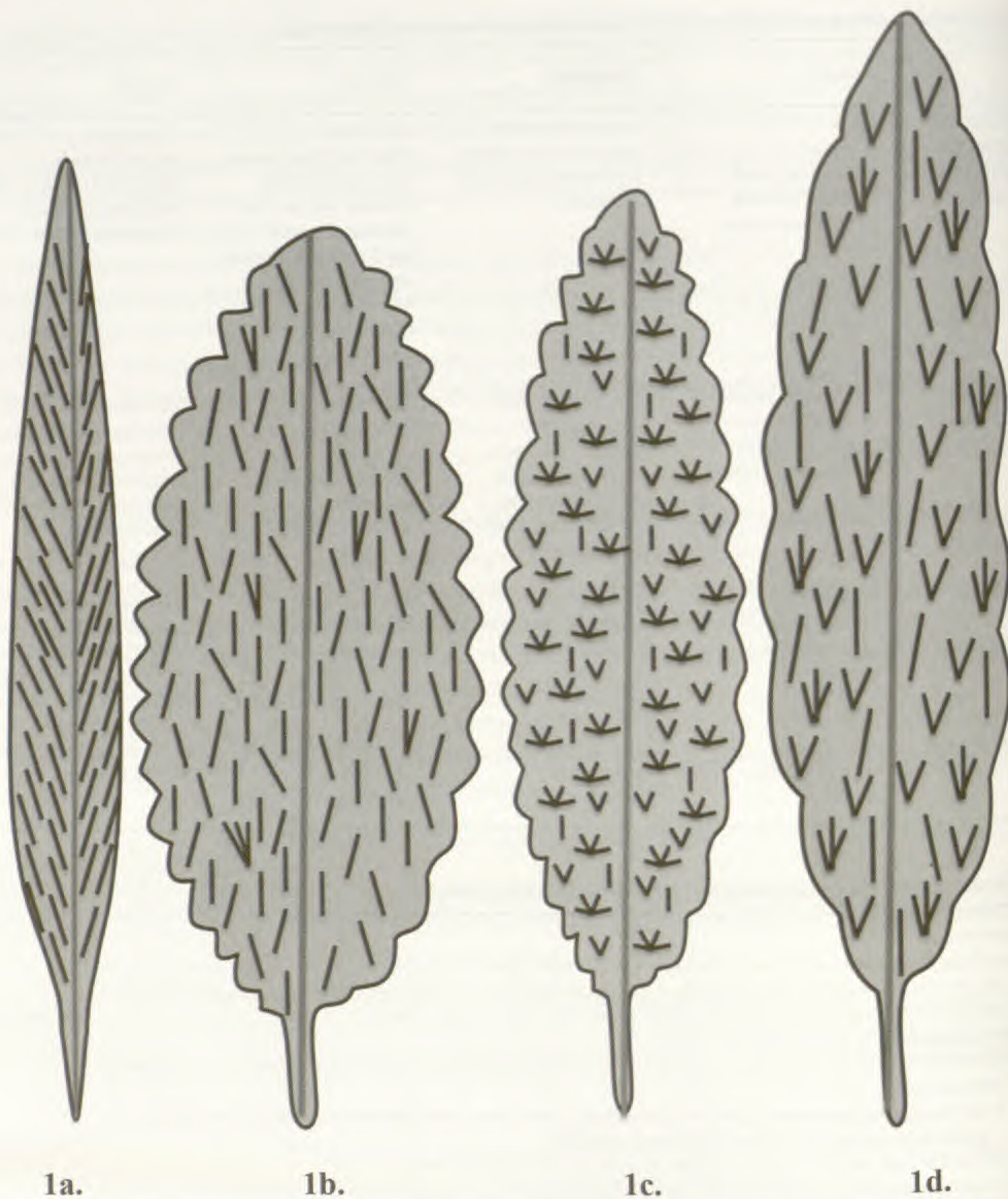


FIG. 1. Graphic representation of the variation in adaxial leaf surface hair types. **1a** represents *Varronia revoluta*, **1b** represents *Varronia leucophlyctis*, **1c** represents *Varronia canescens*, and **1d** represents *Varronia scouleri*.

Distribution and habitat.—Endemic to the Galápagos Islands. This species is found among other shrubs and in forests as an understory tree. It is also found on lava flows and rocky soil. It can be found at elevations from near sea level to 1420 m. Specimens have been collected from Fernandina, Floreana, Isabela, Santa Cruz, and Santiago Islands (Fig. 4).

Specimens examined. **ECUADOR. GALÁPAGOS ISLANDS. Fernandina Island:** Apr 1899, R.E. Snodgrass and E. Heller 327 (GH 244027); Apr 1906, Alban Stewart 3177 (CAS 27260, GH 244032); Feb 1964, John R. Hendrickson 56 (CAS 619244); Feb 1964, F.R. Fosberg 45099 (CAS 749292); Feb 1965, D. Wiens 3825 (CAS 516647); Mar 1967, Inga Eliasson 1700 (S s.n.). **Floreana Island:** Jul 2005, Conley K. McMullen 839 (JMUH 13707); Jul 2005, Conley K. McMullen 838 (JMUH 13705); Jul 2005, Conley K. McMullen 837 (JMUH 13703); Jun 1891, G. Baur 214 (GH 233528); May 1932, John Thomas Howell 9372 (CAS 468109); Feb 1964, Syuzo Itow 189 (CAS 579308); Oct 1905, Alban Stewart 664 (CAS

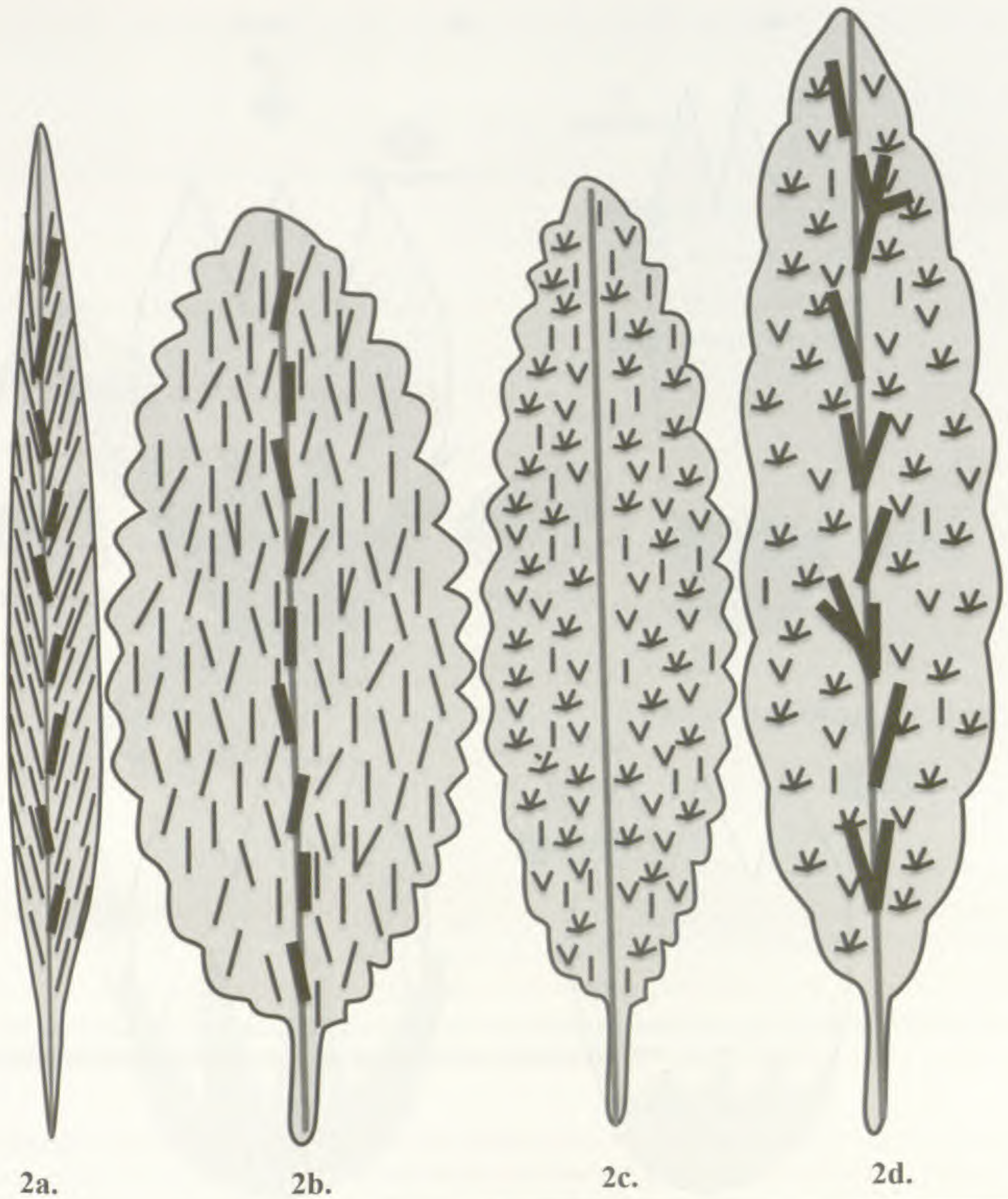


FIG. 2. Graphic representation of the variation in abaxial leaf surface hair types and positioning. **2a** represents *Varronia revoluta*, **2b** represents *Varronia leucophlyctis*, **2c** represents *Varronia canescens*, and **2d** represents *Varronia scouleri*.

694469); Feb 1967, Ira L. Wiggins and Duncan M. Porter 555 (CAS 526365); Oct 1932, H.J.F. Schimpff 215 (BKL 81339, NY s.n.); Dec 1966, Inga Eliasson 785 (KH2007/01159/13, S s.n.); May 1967, Inga Eliasson 2099 (S s.n.); Oct 1932, H.J.F. Schimpff 215 (S s.n.). **Isabela Island:** Aug 2005, Conley K. McMullen 850 (JMUH 13729); Aug 2005, Conley K. McMullen 851 (JMUH 13732); Aug 2005, Conley K. McMullen 852 (JMUH 13734); Aug 2005, Conley K. McMullen 853 (JMUH 13736); Aug 2005, Conley K. McMullen 860 (JMUH 13750); Aug 2005, Conley K. McMullen 861 (JMUH 13752); Aug 2005, Conley K. McMullen 862 (JMUH 13754); Aug 2005, Conley K. McMullen 863 (JMUH 13756); Aug 2005, Conley K. McMullen 849 (JMUH 849); Aug 2005, Conley K. McMullen 848 (JMUH 13725); Jul 1891, G. Baur 213 (GH 233529); Aug 1905, Alban Stewart 3170 (GH 244034); Mar 1932, John Thomas Howell 9465 (GH 244020); Jan 1967, Ira L. Wiggins and Duncan M. Porter 207 (GH 244021); Jan 1899, R.E. Snodgrass and E. Heller 155 (GH 244022); Mar 1899, R.E. Snodgrass and E. Heller 196 (GH 244023); Feb 1899, R.E. Snodgrass and E. Heller 272 (GH 244028); Aug 1905, Alban Stewart 3169 (GH 244025); Mar 1906, Alban Stewart 3173 (GH 244031); Jul 1891, G. Baur 213 (GH 244035); Nov 1905, Alban Stewart 3172 (GH 244033); Jun 1899, R.E. Snodgrass and E. Heller 897 (GH 244030); Dec 1898, R.E. Snodgrass and

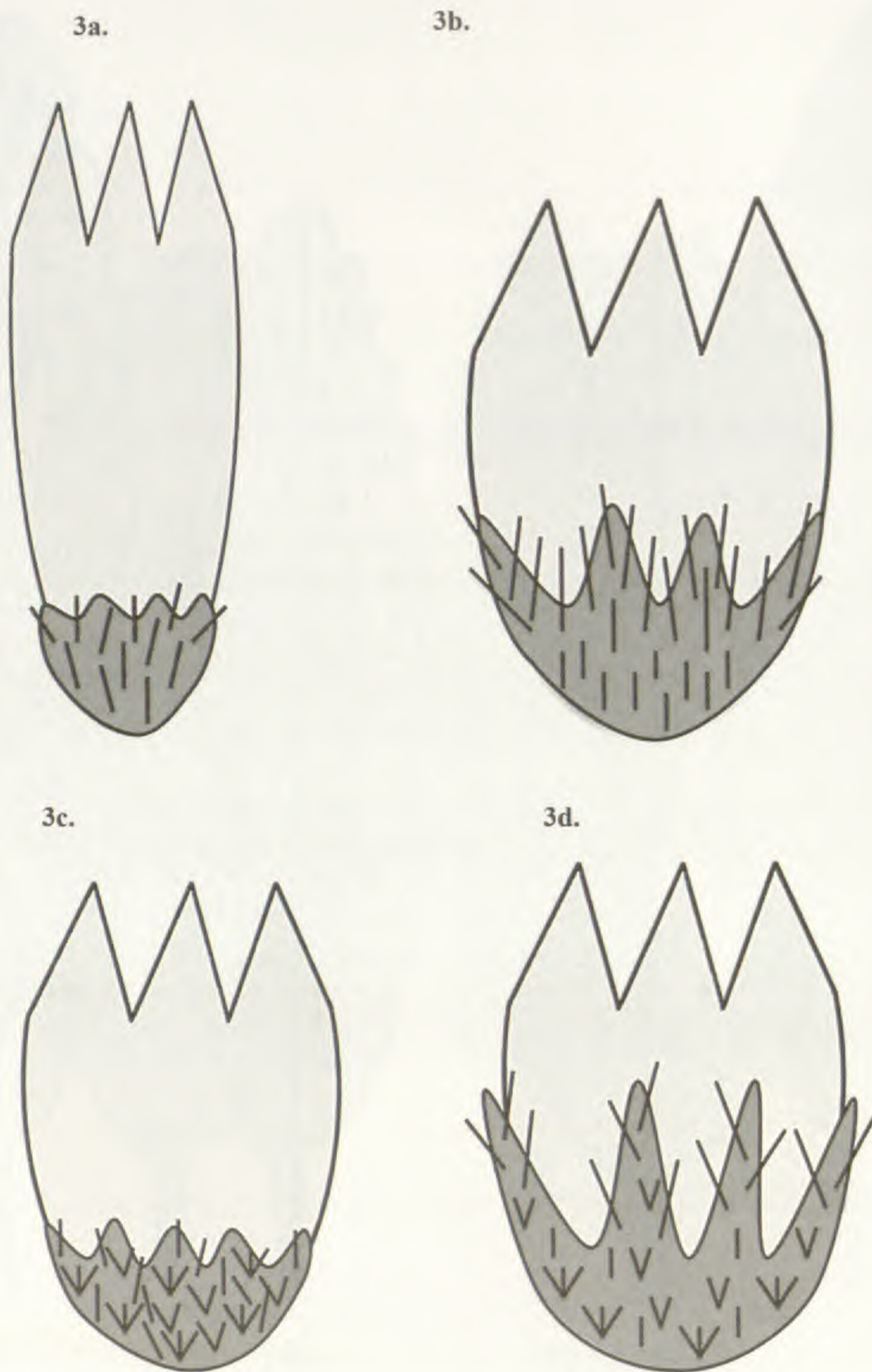


FIG. 3. Graphic representation of the variation in calyx lobe length in comparison to calyx tube length, and variation in calyx hair types. **3a** represents *Varronia revoluta*, **3b** represents *Varronia leucophlyctis*, **3c** represents *Varronia canescens*, and **3d** represents *Varronia scouleri*.

E. Heller 28 (GH 244019); Aug 1905, Alban Stewart 3170 (CAS 27261); Apr 1974, H.H. van der Werff 1025 (CAS 606128); Sep 1975, H.H. van der Werff 2332 (CAS 606129); Jun 1963, David Snow 289 (CAS 579303); Jan 1967, Ira L. Wiggins and Duncan M. Porter 207 (CAS 525322); Jan 1967, Ira L. Wiggins and Duncan M. Porter 231 (CAS 525339); May 1967, Inga Eliasson 2196 (S s.n.); May 1967, Inga Eliasson 2173 (S s.n.); Apr 1967, Inga Eliasson 2013 (S s.n.); Mar 1967, Inga Eliasson 1711 (S s.n.); Mar 1967, Inga Eliasson 1548 (S s.n.); Feb 1967, Inga Eliasson 1305 (S s.n.); Jun 1959, Gunnar Harling 5357 (S s.n.); Jun 1959, Gunnar Harling 5385 (S s.n.); 1825, James Macrae s.n. (K 449167); 1825, James Macrae s.n. (K 449166); Sep 1975, H.H. van der Werff 2332, (K H2007/01159/14). **Santa Cruz Island:** May 1932, John Thomas Howell 9465 (NY s.n.). **Santiago Island:** Jul 1905, Alban Stewart 3176 (GH 244026); Dec 1905, Alban Stewart 3175 (GH 244024); Dec 1905, Alban Stewart 3175 (CAS 27257); Oct 1835, Charles Darwin s.n. (K 449161); Oct 1835, Charles Darwin s.n. (K 449162).

Nomenclatural history.—*Varronia revoluta* is the most distinct of the four endemic *Varronia* species found on

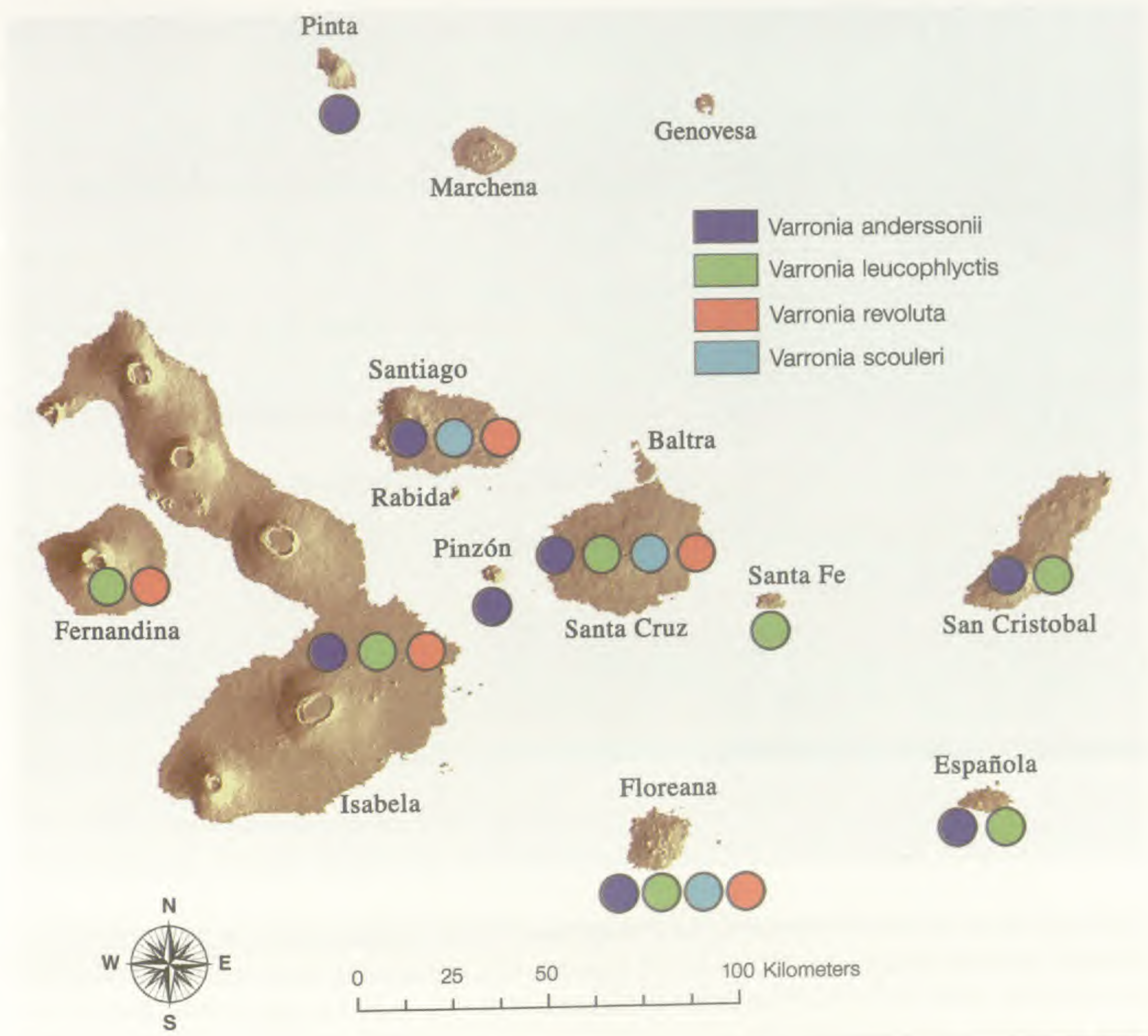


FIG. 4. Distribution of the four endemic *Varronia* species on the Galápagos Islands. The dots represent on which islands an individual species can be found, rather than a specific distribution on each island. No collections have been recorded for Marchena or Genovesa Islands.

the Galápagos Islands. Hooker first described this species in 1847 as *Cordia revoluta* Hook. f. In the same publication, Hooker also described *Cordia revoluta* Hook. f. var. *nigricans* Hook. f. and *Cordia linearis* Hook. f. Because *Cordia linearis* A.DC. was named in 1845, two years before Hooker, Hooker's *C. linearis* is not a validly published name (see Art. 45.3 and Art. 53.1, McNeill et al. 2006). Porter (1980) reviewed old specimens from Hooker, and though he did not discuss the taxonomy, he named *Macrae* s.n. (K 449166) as the lectotype of *Cordia revoluta* Hook. f. var. *nigricans* Hook. f. In observing this specimen, no obvious differences could be found between it and the other types, and it is therefore treated as a synonym in this study. Andersson (1855) transferred *C. revoluta* Hook. f. and *C. linearis* Hook. f. into *Varronia*. In 1891, Kuntze transferred *V. revoluta* (Hook. f.) Anderss. into *Lithocardium*, and in the same publication named a new species, *Lithocardium hookerianum* Kuntze. The type specimen for *L. hookerianum* Kuntze, which was housed in Leipzig (LZ), cannot be located and is presumed to have been destroyed with the herbarium in 1943 during a bombing raid in World War II (Thiers 2012). Gürke (1893) later transferred *L. hookerianum* into *Cordia*. In 1933, Friesen transferred *V. linearis* (Hook. f.) Anderss. and *C. revoluta* Hook. f. into *Sebestena*, without regard to Andersson's earlier renaming of *C. revoluta* Hook. f. as *V. revoluta* (Hook. f.) Anderss. and Kuntze's later reclassification to *Lithocardium revolutum* (Hook. f.) Kuntze. More recently Borhidi (1988) moved *Cordia revoluta* Hook. f. back into *Varronia* as



FIG. 5. View of a typical *Varronia revoluta* shrub displaying characteristic linear leaves and tubular flowers. Photograph courtesy of Conley K. McMullen. Specimen: Aug 2005, Conley K. McMullen, 848 (JMUH 13725).

V. revoluta (Hook. f.) Borhidi without regard to Andersson's (1855) original nomenclature for the species. Therefore, Borhidi's change is invalid (see Art. 45.3 and Art. 53.1, McNeill et al. 2006). Recently, *Varronia* was resurrected by Miller and Gottschling (2007) and because of this, the name *Varronia revoluta* (Hook. f.) Andersson has priority as the species name.

Contribution of this study.—After examining the types and other specimens, this species has distinctive linear leaves with revolute margins (Fig. 5), separating it from the other three Galápagos *Varronia*. *Varronia revoluta* also has very consistent leaf hairs that do not vary among the specimens examined. Adaxial leaf surfaces are densely pubescent with distinctive white, simple hairs that are appressed with tips oriented towards the leaf apex and/or outer margins (Fig. 6). Abaxial leaf surfaces also have simple, dense hairs. Margins are villous pubescent with simple hairs. More robust, appressed white hairs are found on the veins, which also bend towards the leaf apex/outer margins (Fig. 7). Calyxes are densely villous with simple hairs which are a uniform length throughout the entirety of the calyx. Calyx lobes are much shorter than the calyx tube at anthesis. The characters observed in this study agree with the description reported by Wiggins and Porter (1971). However, this study provides a more complete description of the leaf hairs, which are deemed to be the distinguishing features among the other three endemic Galápagos *Varronia* species.

2. *Varronia leucophlyctis* (Hook. f.) Andersson, Kongl. Vetensk.-Akad. Handl. 1853:203. 1855. \equiv *Cordia leucophlyctis* Hook. f., Trans. Linn. Soc. London 20:199. 1847. TYPE: ECUADOR. GALÁPAGOS ISLANDS. Albemarle Island (Isabela Island): 1835, Charles Darwin s.n. (LECTOTYPE, designated by Porter 1980: CGE 00285). PARALECTOTYPES: ECUADOR. GALÁPAGOS ISLANDS. Albemarle Island (Isabela Island): 1825, Macrae s.n. (Porter 1980, K 449164!); no date, Macrae s.n. (Porter 1980, K 449163!). \equiv *Lithocardium leucophlyctis* (Hook. f.) Kuntze, Revis. Gen. Pl. 2:977. 1891.

\equiv *Varronia scaberrima* Andersson, Kongl. Vetensk.-Akad. Handl. 1853:202. 1855, nom. illeg. TYPE: ECUADOR. GALÁPAGOS ISLANDS. Indefatigable Island (Santa Cruz Island): 1853, Andersson 220 (HOLOTYPE: S 04-2351). \equiv *Lithocardium galapagosenum* Kuntze, Revis. Gen. Pl. 2:976. 1891. \equiv *Cordia galapagensis* (Kuntze) Gürke, Nat. Pflanzenfam. 4(3):83. 1893.

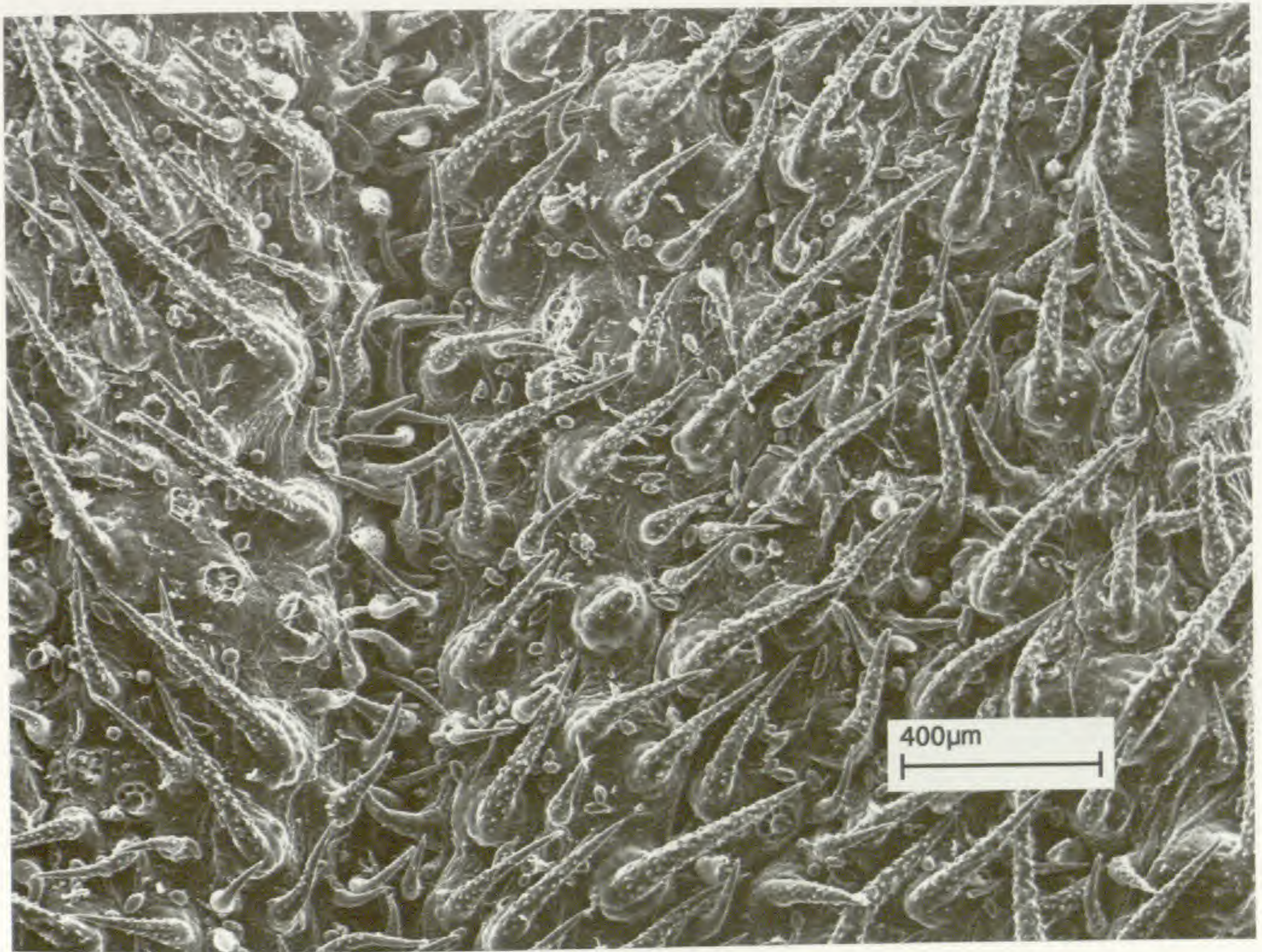


FIG. 6. *Varronia revoluta* adaxial leaf surface displaying typical large, appressed simple hairs. Scale represents 400 μm . Specimen: Jul 2005, Conley K. McMullen, 838 (JMUH 13705).

Species description.—*Varronia leucophlyctis* is an open shrub 1.0–2.5 m tall, with one to several erect to ascending stems; bark dark brownish gray, with scattered, reddish tan, almost circular lenticels; young twigs, petioles, and peduncles densely pubescent with simple hairs (Wiggins & Porter 1971). Leaves broadly lanceolate, 2.0–11.0 cm long, 0.8–4.0 cm wide, with finely serrate to crenate margins; adaxial leaf surfaces dark green, pubescent with mostly erect and simple hairs (Fig. 1b); abaxial leaf surfaces lighter green, often densely pubescent with mostly erect and simple hairs (Fig. 2b). Inflorescence capitate, with erect, mostly simple hairs; simple hairs on veins are commonly robust (Fig. 2b). Calyx broadly cup-tate to short-spicate, on terminal peduncles 1.0–5.0 cm long (Wiggins & Porter 1971). Calyx broadly cup-shaped to narrowly campanulate, 6.0 mm long, 4.0 mm wide, 4- or 5-lobed (Wiggins & Porter 1971); calyx lobes about as long as calyx tube at anthesis (Fig. 3b); calyx pubescent with erect and simple hairs that are noticeably longer on calyx lobes than calyx tube (Fig. 3b). Corolla white, usually 5-lobed, funnellform, tube 7.0–8.0 mm long, 7.0–8.0 mm wide; lobes rotate-spreading to slightly reflexed (Wiggins & Porter 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

Distribution and habitat.—Endemic to the Galápagos Islands. This species is found among lava boulders and in rocky soil among other shrubs. It is also sometimes found as an understory shrub in forested areas. Found from near sea level to 1750 m. Specimens have been collected from Española, Fernandina, Floreana, Isabela, San Cristobal, Santa Cruz, and Santa Fe Islands (Fig. 4).

Specimens examined. **ECUADOR. GALÁPAGOS ISLANDS. Española Island:** Feb 1906, Alban Stewart 3168 (GH 244016); Feb 1906, Alban Stewart 3168 (CAS 27273). **Fernandina Island:** Mar 1899, R.E. Snodgrass and E. Heller 342 (CAS 9251, GH 244008); Apr 1899, R.E. Snodgrass and E. Heller 331 (GH 233533); Mar 1967, Inga Eliasson 1701 (S s.n.); Sep 1972, A.E.P. Schmidt 2535 (C 24/2007/26); Jan 1972, Michelle and Ole Hamann 222 (C 24/2007/22). **Floreana Island:** Jul 2005, Conley K. McMullen 840 (JMUH 13708); Jul 2005, Conley K. McMullen 844 (JMUH

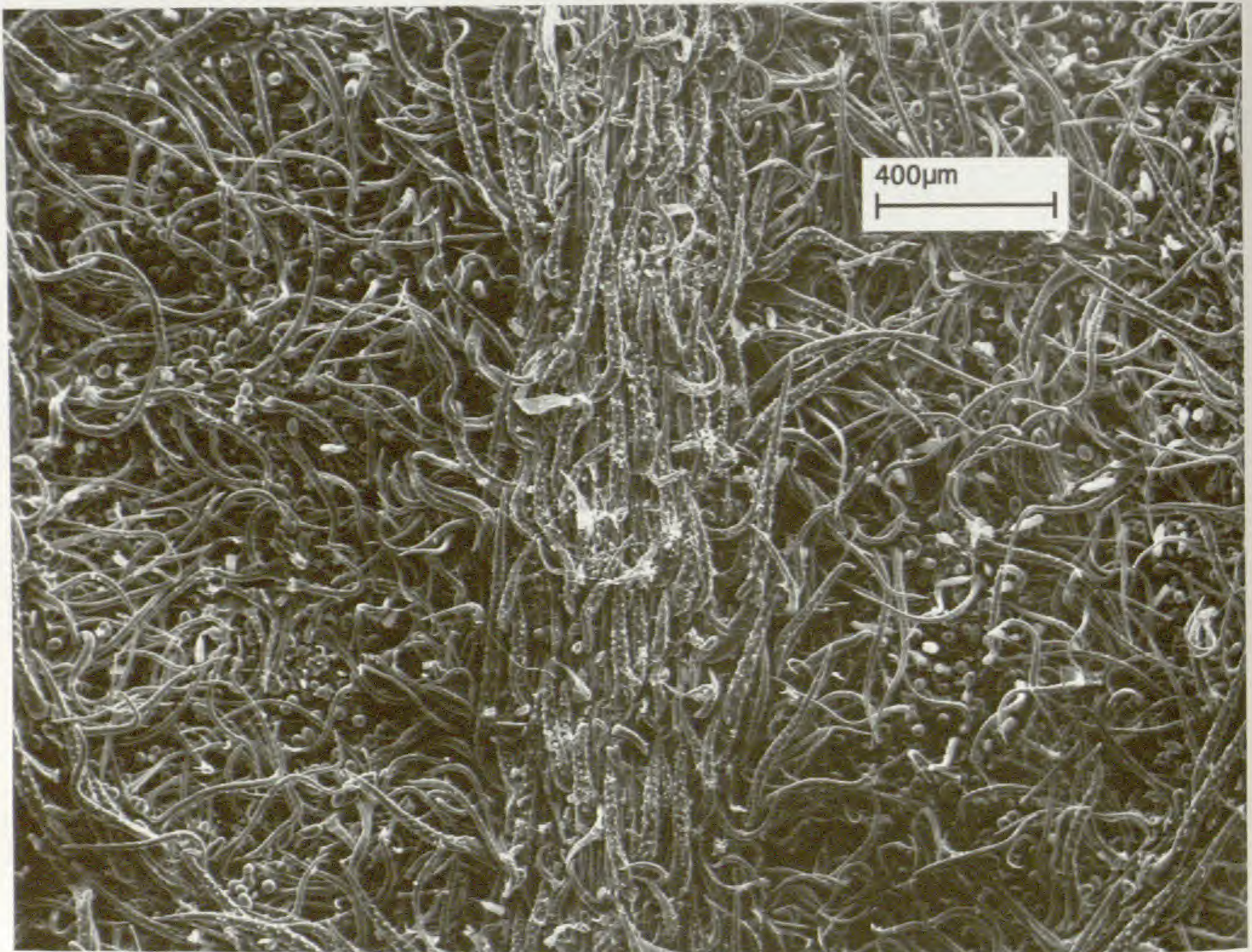


FIG. 7. *Varronia revoluta* abaxial leaf surface displaying robust appressed simple hairs on veins, and densely villous simple hairs in margins. Scale represents 400 μm . Specimen: Jul 2005, Conley K. McMullen, 838 (JMUH 13705).

13716); Dec 1966, Inga Eliasson 824 (S s.n.); Dec 1966, Inga Eliasson 813 (S s.n.); Dec 1966, Inga Eliasson 904 (S s.n.); Dec 1966, Inga Eliasson 877 (S s.n.). **Isabela Island:** Aug 2005, Conley K. McMullen 859 (JMUH 13748); Aug 2005, Conley K. McMullen 857 (JMUH 13745); Aug 2005, Conley K. McMullen 856 (JMUH 13743); Aug 2005, Conley K. McMullen 858 (JMUH 13747); Aug 2005, Conley K. McMullen 854 (JMUH 13739); Mar 2007, Conley K. McMullen and Michael Shane Woolf 881 (JMUH 13797); Mar 2007, Conley K. McMullen and Michael Shane Woolf 877 (JMUH 13788); Mar 2007, Conley K. McMullen and Michael Shane Woolf 878 (JMUH 13790); Mar 2007, Conley K. McMullen and Michael Shane Woolf 879 (JMUH 13792); Mar 2007, Conley K. McMullen and Michael Shane Woolf 880 (JMUH 13794); Mar 1906, Alban Stewart 3159 (GH 244014); Mar 1906, Alban Stewart 3164 (GH 233526); Mar 1899, R.E. Snodgrass and E. Heller 195 (GH 244007); Feb 1899, R.E. Snodgrass and E. Heller 291 (GH 233534); Jun 1899, R.E. Snodgrass and E. Heller 893 (CAS 9260, GH 244011); Jun 1899, R.E. Snodgrass and E. Heller 857 (GH 244013); Jun 1899, R.E. Snodgrass and E. Heller 881 (GH 244012); Aug 1891, G. Baur 212 (GH 233532); Jul 1891, G. Baur 210 (GH 233530); no date, R.E. Snodgrass and E. Heller 136 (GH 244009); Dec 1898, R.E. Snodgrass and E. Heller 75 (GH 244010); Apr 1932, John Thomas Howell 8976 (CAS 468107); Mar 1906, Alban Stewart 3161 (CAS 27270); Jan 1967, Ira L. Wiggins and Duncan M. Porter 232 (K H2007/01159/9, CAS 525340); Mar 1906, Alban Stewart 3160 (CAS 27272); May 1932, John Thomas Howell s.n. (CAS 468103); May 1932, John Thomas Howell 9431 (CAS 468111); Apr 1974, H.H. van der Werff 1037 (CAS 606063); Apr 1974, H.H. van der Werff 1033 (CAS 606062); Jun 1959, Gunnar Harling 5622 (S s.n.); Jun 1959, Gunnar Harling 5360 (S s.n.); Jun 1959, Gunnar Harling 5312 (S s.n.); Apr 1967, Inga Eliasson 2034 (S s.n.); Mar 1967, Inga Eliasson 1713 (S s.n.); May 1967, Inga Eliasson 2219 (S s.n.); May 1967, Inga Eliasson 2208 (S s.n.); Feb 1967, Inga Eliasson 1285 (S s.n.); Feb 1967, Inga Eliasson 1303 (S s.n.); Sep 1972, Michelle and Ole Hamann 2243 (C 24/2007/24); Jul 1972, Michelle and Ole Hamann 1780 (C 24/2007/20); Jul 1972, Michelle and Ole Hamann 1771 (C 24/2007/19); Jul 1972, Michelle and Ole Hamann 1709 (C 24/2007/18); Jul 1972, Michelle and Ole Hamann 1615 (C 24/2007/17); Sep 1972, Michelle and Ole Hamann 2320 (C 24/2007/12); 1825, James Macrae s.n. (K 449163); 1825, James Macrae s.n. (K 449164); Apr 1932, John Thomas Howell 8976 (K H2007/01159/15). **San Cristobal Island:** Feb 1967, Ira L. Wiggins and Duncan M. Porter 379 (CAS 526675, GH 233549). **Santa Cruz Island:** Apr 1930, H.K. Svenson 7 (GH 233525-1); Feb 1964, Ira L. Wiggins 18485 (CAS 619426, GH 244006); Aug 1891, G. Baur 211 (GH 233531); Mar 1938, C.M. Haggis 21 (CAS 262726); Mar 1935, J.P. Chapin 1125 (BKL 81351, NY s.n.); May 1981, C. Grady Walker 568 (NY s.n.); Apr 1967, Inga Eliasson 1940 (S s.n.); Apr 1967, Inga Eliasson 1919 (S s.n.); Nov 1966, Inga Eliasson 514 (S s.n.); Apr 1972, P. Pritchard 1197 (C 24/2007/13); Mar 1981, O. Hamann and O. Seberg 1772b (C 24/2007/16); Mar



FIG. 8. View of a typical *Varronia leucophlyctis* lanceolate leaf with crenate margins. Photograph courtesy of Conley K. McMullen. Specimen: Mar 2007, Conley K McMullen and Michael Shane Woolf, 881 (JMUH 13797).

1981, O. Seberg 1746 (C 24/2007/15). **Santa Fe Island:** Oct 1905, Alban Stewart 3164 (CAS 27266, GH 244015); Feb 1972, Michelle and Ole Hamann 463 (C 24/2007/21).

Nomenclatural history.—Hooker (1847) first described this species as *Cordia leucophlyctis* Hook. f., moved by Andersson (1855) into *Varronia*, then transferred into *Lithocardium* by Kuntze (1891). In 1855, Andersson described a new species, *Varronia scaberrima* Andersson; however, as *Varronia scaberrima* Bert. ex Spreng. was already in existence, *V. scaberrima* Andersson is not valid (see Art. 45.3 and Art. 53.1, McNeill et al. 2006). In 1891, Kuntze moved both *Varronia* P. Br. and *Cordia* L. into *Lithocardium* Kuntze; however, Kuntze renamed *V. scaberrima* as *Lithocardium galapagosenum* Kuntze, because the epithet “*scaberrima*” was already occupied by *L. scaberrima*, which had priority. *Lithocardium galapagosenum* was later moved by Gürke (1893) into *Cordia*, and was considered taxonomically synonymous to *Cordia leucophlyctis* by Wiggins and Porter (1971). Miller and Gottschling’s (2007) resurrection of the genus *Varronia* makes *Varronia leucophlyctis* (Hook. f.) Andersson the correctly recognized name for this species.

Contribution of this study.—The leaves of *V. leucophlyctis* tend to be distinct from those of either *V. canescens* or *V. scouleri*. The leaf shape tends to be broadly lanceolate with finely serrate to crenate margins (Fig. 8), but this is not entirely consistent among the specimens examined. However, as with *V. revoluta*, *V. leucophlyctis* has mostly consistent hair types across all of the examined specimens. Adaxial leaf surface hairs are mostly erect and simple (Fig. 9). Abaxial leaf surfaces are often densely pubescent, with mostly simple, erect hairs; simple, larger hairs can be found on the veins (Fig. 10). Very rarely, forked or stellate hairs may be found on either leaf surface of *V. leucophlyctis*. Calyx hairs are also erect and simple, and noticeably longer on the calyx lobes than on the calyx tube. The calyx lobes themselves are about as long as the calyx tube at anthesis.

Though leaf morphology of this species is often distinct, *V. leucophlyctis* can still be confused with both *V. canescens* and *V. scouleri*. In this situation, the hairs on the adaxial and abaxial leaf surfaces are the best char-

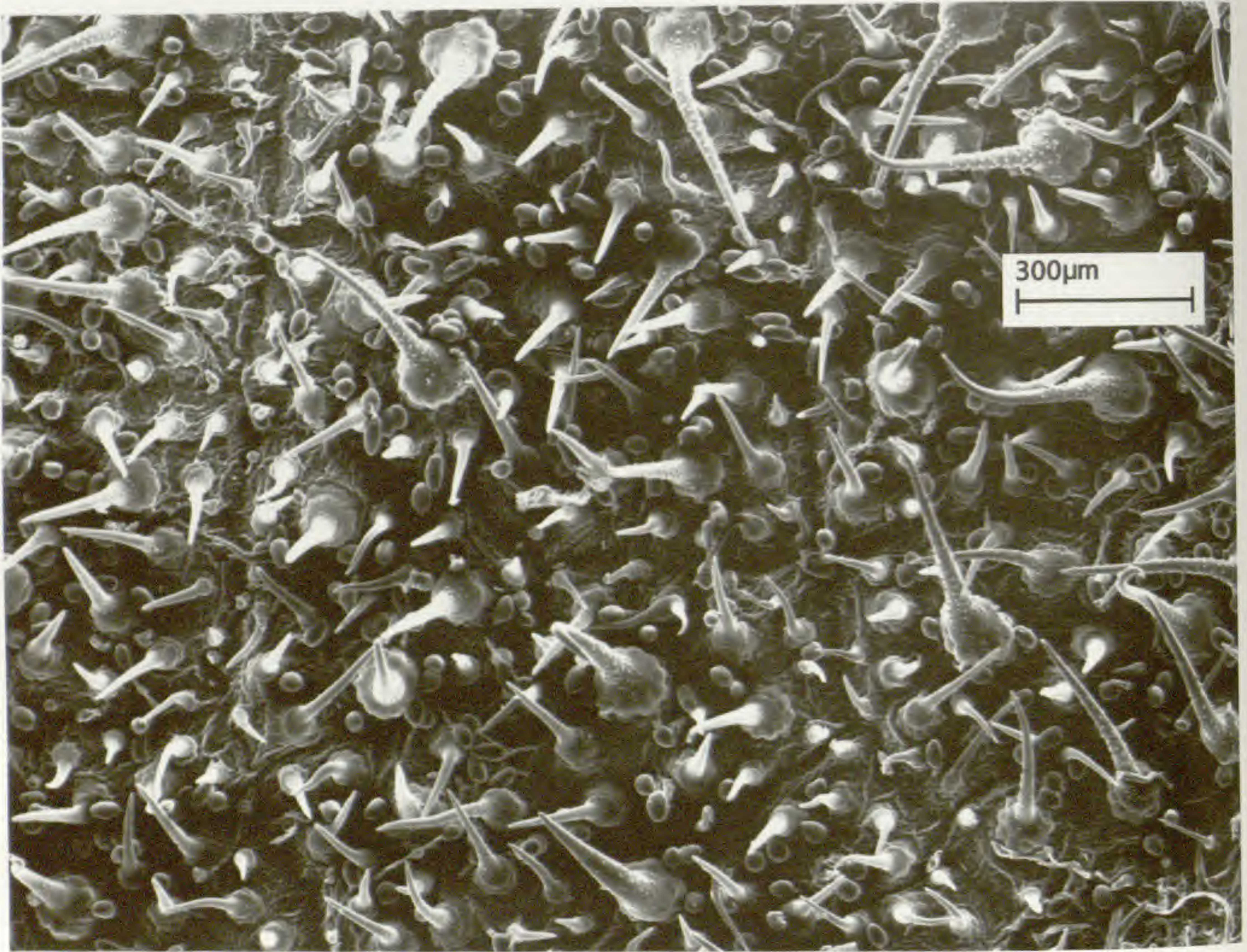


FIG. 9. *Varronia leucophlyctis* adaxial leaf surface displaying erect, simple hairs. Scale represents 300 μm . Specimen: Jul 2005, Conley K. McMullen, 844 (JMUH 13716).

acter to use for identification. Neither *V. canescens* nor *V. scouleri* possesses predominately simple, erect hairs on both leaf surfaces, and in the same abundance as found on *V. leucophlyctis*.

3. *Varronia canescens* Andersson, Kongl. Vetensk.-Akad. Handl. 1853:203. 1855. TYPE: ECUADOR. GALAPAGOS ISLANDS. Charles Island (Floreana Island): 1853, Andersson s.n. (HOLOTYPE: S 04-1959!).

= *Lithocardium anderssonii* Kuntze, Revis. Gen. Pl. 2:976. 1891. \equiv *Cordia anderssonii* (Kuntze) Gürke, Nat. Pflanzenfam. 4(3):83. 1893. \equiv *Varronia anderssonii* (Kuntze) Borhidi, Acta Bot. Hung. 34:383. 1988, nom. illeg.

Species description.—*Varronia canescens* is an erect, moderately branched shrub 1.0–3.0 m tall, with one to several stems from the base; bark dark brown and thin (Wiggins & Porter 1971). Young twigs densely pubescent with appressed stellate, forked, and simple hairs. Leaves lanceolate, 1.3–11.8 cm long, 0.5–4.3 cm wide, with finely serrate to crenate margins; adaxial leaf surfaces dark green, glabrous to sparsely pubescent with hairs typically appressed or sometimes weakly erect, stellate and forked, sometimes simple (Fig. 1c); abaxial leaf surfaces lighter green, densely pubescent with appressed stellate, forked, and simple hairs (Fig. 2c). Inflorescence subcapitate to short-spicate, on slender peduncles, 1.5–10.0 cm long (Wiggins & Porter 1971). Calyx narrowly campanulate, 3.0–5.0 mm long, 4- or 5-lobed (Wiggins & Porter 1971); calyx lobes as long as or shorter than calyx tube at anthesis (Fig. 3c); calyx appressed pubescent with stellate, forked, and simple hairs, generally uniform length throughout (Fig. 3c). Corolla white, 5-lobed, funnellform, tube 5.0–8.0 mm at anthesis, lobes rotate-spreading to reflexed (Wiggins & Porter 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

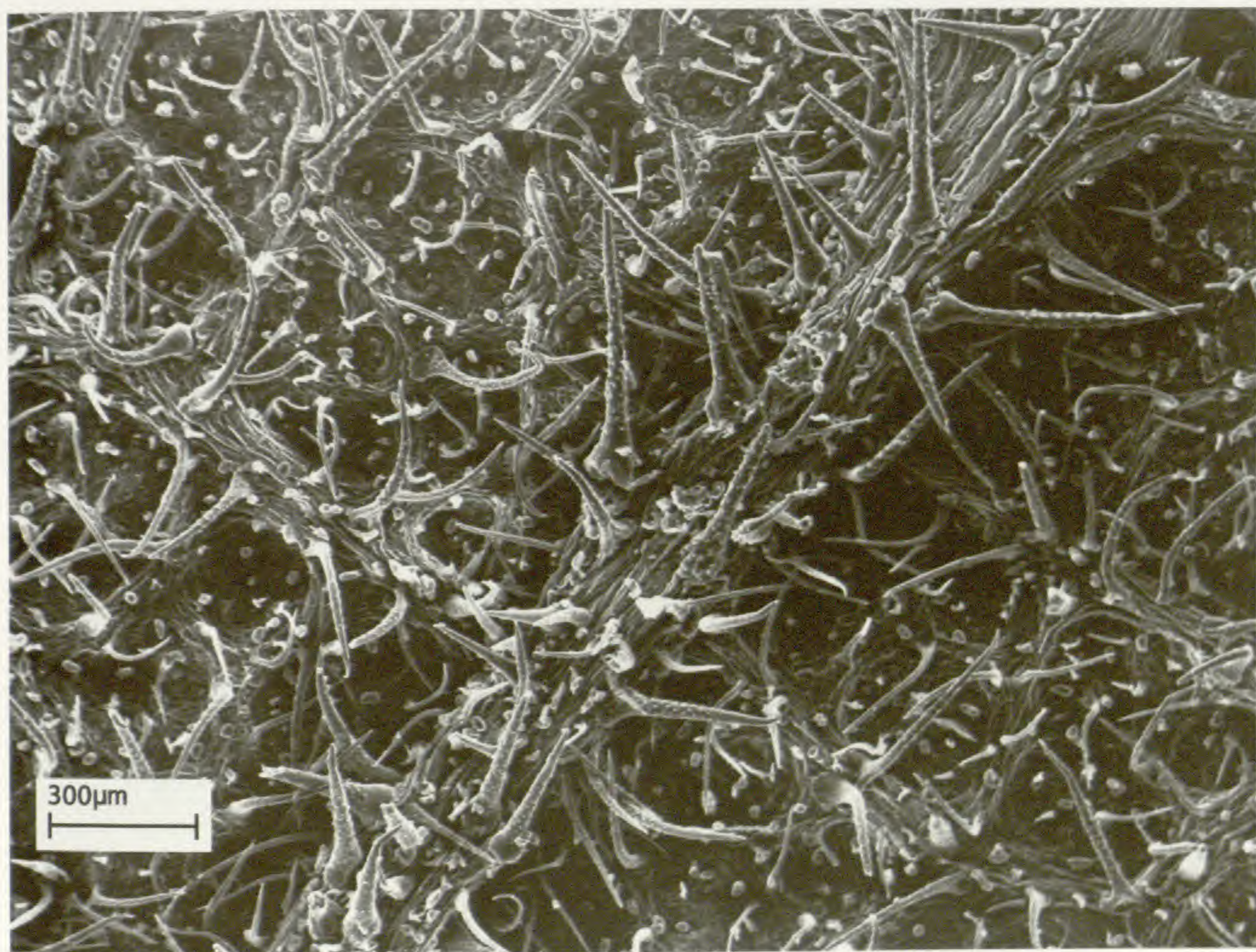


FIG. 10. *Varronia leucophlyctis* abaxial leaf surface displaying robust, erect simple hairs on veins, and simple hairs in margins. Scale represents 300 μm . Specimen: Mar 2007, Conley K. McMullen and Michael Shane Woolf, 880 (JMUH 13794).

Distribution and habitat.—Endemic to the Galápagos Islands. This species is found among lava boulders and in rocky soil among other shrubs. It is also sometimes found as an understory shrub in forested areas. Found from near sea level to 950 m. Specimens have been collected from Española, Floreana, Isabela, Pinta, Pinzón, San Cristobal, Santa Cruz, and Santiago Islands (Fig. 4). This species is the most widely distributed of the endemic Galápagos *Varronia*.

Specimens examined. **ECUADOR. GALÁPAGOS ISLANDS. Española Island:** Feb 1964, C.B. Koford 24 (CAS 619350); Apr 1932, John Thomas Howell 8706 (CAS 468106). **Floreana Island:** Jul 2005, Conley K. McMullen 841 (JMUH 13710); Jul 2005, Conley K. McMullen 842 (JMUH 13712); Jul 2005, Conley K. McMullen 843 (JMUH 13714); 1853, Andersson s.n. (GH 233538); Apr 1888, Leslie A. Lee s.n. (GH 233547); 1853, Andersson s.n. (S 504-1959); Dec 1966, Inga Eliasson 826 (S s.n.); Jun 1972, Michelle and Ole Hamann 1423 (C 24/2007/10). **Isabela Island:** Aug 1905, Alban Stewart 3195 (CAS 27276, GH 233543, NY s.n.). **Pinta Island:** Sep 1905, Alban Stewart 3158 (CAS 27267, GH 233542); Mar 1972, Michelle and Ole Hamann 869 (C 24/2007/6); Mar 1972, Michelle and Ole Hamann 920 (C 24/2007/1); May 1964, David Snow 589 (K H2007/01159/16); 1868, Habel s.n. (K H2007/01159/17). **Pinzón Island:** Aug 1891, G. Baur 215 (GH 244002); May 1970, Syuzo Itow 51409-1 (CAS 623521); Aug 1905, Alban Stewart 3167 (CAS 27274); Jan 1967, Inga Eliasson 1046 (S s.n.); Jan 1967, Inga Eliasson 1042 (S s.n.); May 1972, Michelle and Ole Hamann 1250 (C 24/2007/5). **San Cristobal Island:** Mar 2007, Conley K. McMullen and Michael Shane Woolf 882 (JMUH 13799); Mar 2007, Conley K. McMullen and Michael Shane Woolf 883 (JMUH 13802); Mar 2007, Conley K. McMullen and Michael Shane Woolf 884 (JMUH 13804); Mar 2007, Conley K. McMullen and Michael Shane Woolf 885 (JMUH 13806); Mar 2007, Conley K. McMullen and Michael Shane Woolf 886 (JMUH 13809); Jul 2005, Conley K. McMullen 830 (JMUH 13688); Jul 2005, Conley K. McMullen 824 (JMUH 13675); Jul 2005, Conley K. McMullen 825 (JMUH 13677); Jul 2005, Conley K. McMullen 826 (JMUH 13679); Jul 2005, Conley K. McMullen 827 (JMUH 13681); Jul 2005, Conley K. McMullen 828 (JMUH 13684); Jul 2005, Conley K. McMullen 829 (JMUH 13685); Jun 1891, G. Baur 216 (GH 233523); no date, Andersson s.n. (GH 233539); Feb 1906, Alban Stewart 3165 (CAS 27265, GH 233540); Feb 1906, Alban Stewart 3166 (GH 233541); no date, F. Fagerlind and G. Wibom s.n. (S s.n.); no date, F. Fagerlind and G. Wibom 2753 (S s.n.); Apr 1967, Inga Eliasson 1848 (S s.n.); no date, Andersson s.n. (S s.n.); no date, Andersson 222 (S s.n.); 1853, Andersson s.n. (S s.n.); Jun 1959, Gunnar Harling 5652 (S s.n.). **Santa Cruz**



FIG. 11. View of typical *Varronia canescens* lanceolate leaves with crenate margins. Photograph courtesy of Conley K. McMullen. Specimen: Mar 2007, Conley K. McMullen and Michael Shane Woolf, 884 (JMUH 13804).

Island: Dec 1966, Inga Eliasson 1000 (S s.n.); Mar 1972, Michelle and Ole Hamann 613 (C 24/2007/25); Dec 1974, H.H. van der Werff 1722 (K H2007/01159/18); Feb 1939, T.W.J. Taylor, G21 (K H2007/01159/10). **Santiago Island:** Jan 1906, Alban Stewart 3154 (GH 233544); Jan 1906, Alban Stewart 3157 (CAS 27255); Jan 1967, Inga Eliasson 1128 (S s.n.); Aug 1972, Michelle and Ole Hamann 2053 (C 24/2007/23); Aug 2005, Conley K. McMullen 870 (JMUH 13770). **Unknown Island:** no date, Andersson 123 (C 24/2007/14, K 449160).

Nomenclatural history.—Andersson first described this species in 1855 as *Varronia canescens* Anderss. In 1891, Kuntze moved both *Varronia* P. Br. and *Cordia* L. into *Lithocardium* Kuntze. However, the epithet “*canescens*” was occupied by *Cordia canescens* Kunth which had priority, so Kuntze (1891) renamed *V. canescens* Anderss. as *Lithocardium anderssonii* Kuntze. Subsequently, Gürke (1893) later reclassified *L. anderssonii* Kuntze as *Cordia*. More recently Borhidi (1988) moved *C. anderssonii* (Kuntze) Gürke back into *Varronia* as *V. anderssonii* (Kuntze) Borhidi without regard to Andersson’s (1855) original nomenclature for the species. Therefore, Borhidi’s change is invalid (see Art. 45.3 and Art. 53.1, McNeill et al. 2006). As such, *V. canescens* Andersson should be considered the correct name for this species based upon Miller and Gottschling’s (2007) reinstatement of genus *Varronia*.

Contribution of this study.—Based on characters observed on the type specimen, this species has lanceolate leaves with finely serrate to crenate margins (Fig. 11), but these characters were variable when observing all herbarium specimens. *Varronia canescens* has a propensity to look most similar to *V. scouleri*, though the leaves of *V. canescens* do not tend to be as long as those found on *V. scouleri*, nor are the leaf margins on *V. canescens* as coarsely serrate as those generally found on *V. scouleri*. The pubescence on the adaxial surface of the leaves of *V. canescens*, when present, is typically appressed (Fig. 12) or weakly erect (Fig. 13) and composed mostly of stellate and forked, occasionally simple hairs. The abaxial leaf surfaces are densely pubescent, with

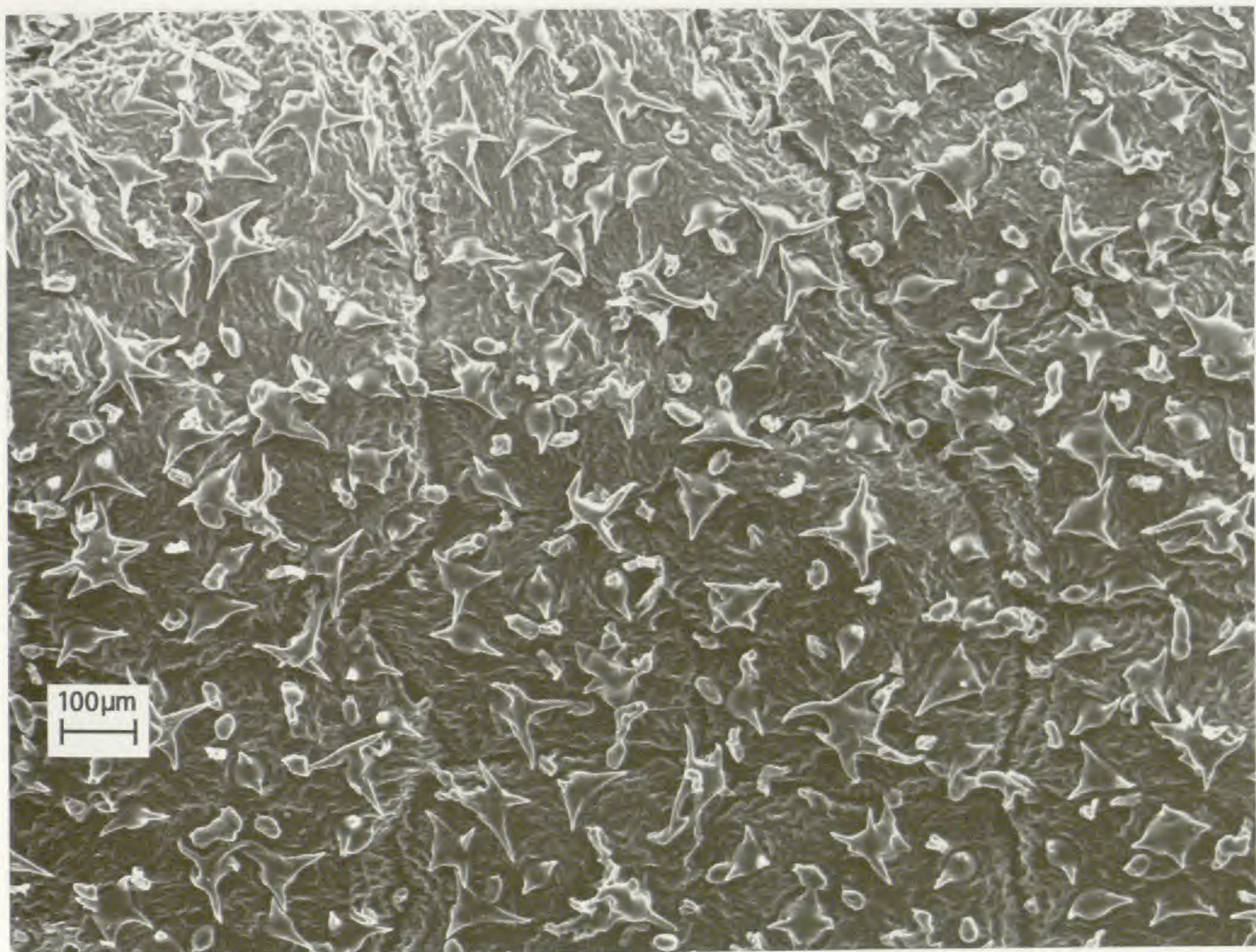


FIG. 12. *Varronia canescens* adaxial leaf surface displaying appressed stellate and forked hairs. Scale represents 100 μm . Specimen: Jul 2005, Conley K. McMullen, 824 (JMUH 13675).

appressed stellate, forked, and simple hairs (Fig. 14). The abaxial pubescence of *V. canescens* is the densest of any of the four endemic species and the most obviously appressed. In addition, the hairs on the veins do not tend to be any larger than those found in the margins, providing another character that distinguishes *V. canescens* from the other three endemic species. The pubescence on the calyx is composed of appressed stellate, forked, and simple hairs, which are a uniform length through the length of the calyx. In contrast to the other species, the hairs are generally very short. The calyx lobes are as long as or shorter than the calyx tube at anthesis.

4. *Varronia scouleri* (Hook. f.) Andersson, Kongl. Vetensk.-Akad. Handl. 1853:204. 1855. \equiv *Cordia scouleri* Hook. f., Trans. Linn. Soc. London 20:200. 1847. TYPE (Porter 1980): ECUADOR. GALÁPAGOS ISLANDS. James Island (Santiago Island): no date, John Scouler s.n. (HOLOTYPE: K 449165!). \equiv *Lithocardium scouleri* (Hook. f.) Kuntze, Revis. Gen. Pl. 2:977. 1891. \equiv *Varronia scouleri* (Hook. f.) Borhidi, Acta Bot. Hung. 34:387. 1988, nom. illeg.

Species description.—*Varronia scouleri* is an ascending branched shrub, with dullish dark gray bark with circular or transversely lenticular lenticels (Wiggins & Porter 1971). Young twigs sparsely pubescent with generally appressed stellate and forked, or sometimes simple hairs. Some noticeably larger, more robust hairs may also be observed. Leaves lanceolate, 2.3–17.5 cm long, 0.5–5.0 cm wide, with coarsely serrate margins; adaxial leaf surfaces dark green and pubescent with erect simple, forked, and sometimes stellate hairs (Fig. 1d); abaxial leaf surfaces lighter green and sparsely pubescent with weakly appressed stellate and forked, sometimes simple hairs which are noticeably more robust on elevated veins (Fig. 2d). Inflorescence globose-capitate, on peduncles 3.0–5.0 mm long (Wiggins & Porter 1971). Calyx globose in bud, campanulate after anthesis, 5-lobed; lobes are 4.0 mm long, excluding elongated slender lobe tips, and 3.0–4.0 mm wide (Wiggins & Porter 1971);

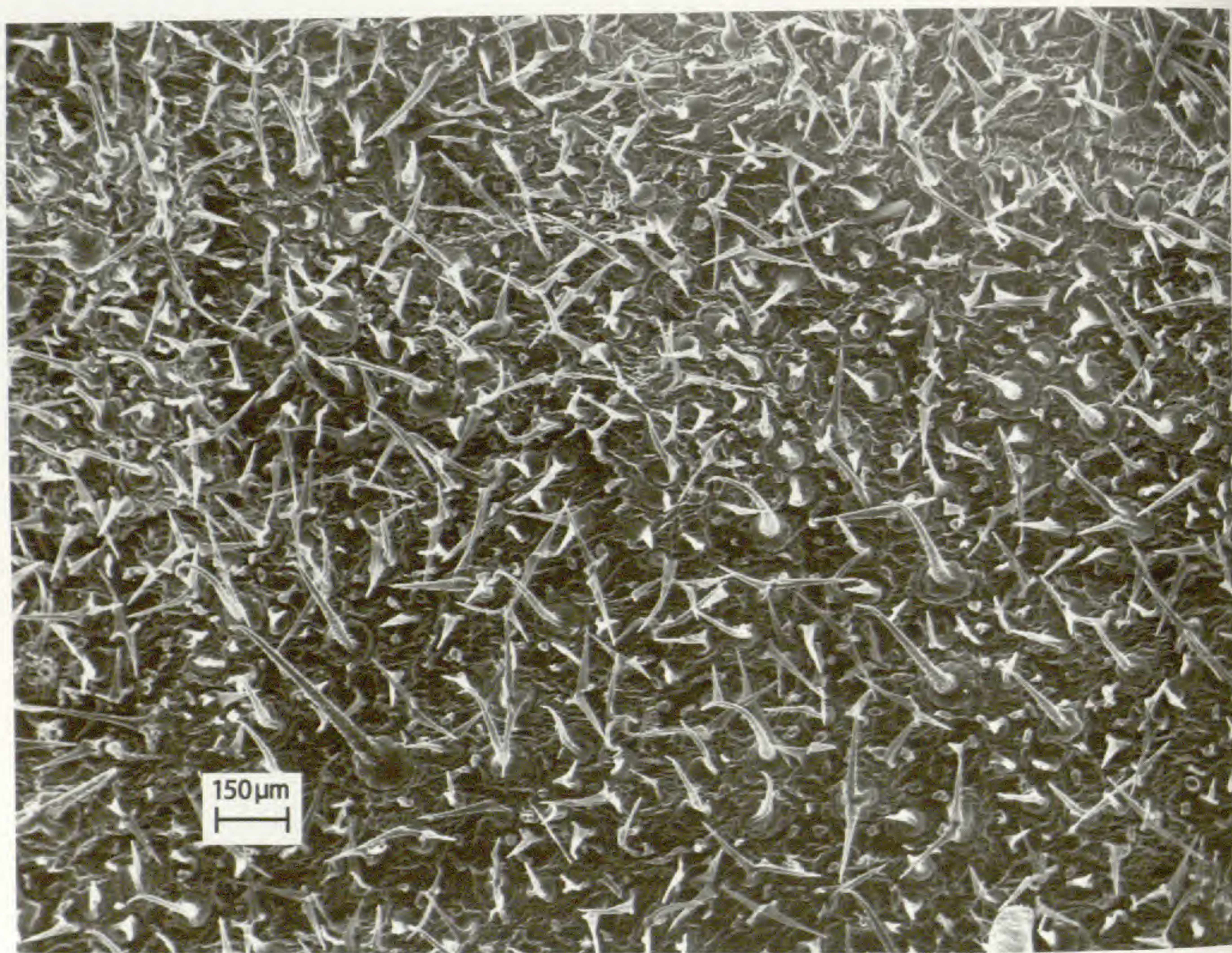


FIG. 13. *Varronia canescens* adaxial leaf surface displaying weakly erect stellate, forked, and simple hairs. Scale represents 150 μm . Specimen: Mar 2007, Conley K. McMullen and Michael Shane Woolf, 884 (JMUH 13804).

elongated lobe tips may be as long as, or longer than the lobe, 4.0–8.0 med mer; calyx lobes usually longer than calyx tube at anthesis (Fig. 3d). Pubescence on the calyx composed of erect and simple, sometimes forked or stellate hairs. Simple hairs noticeably longer on the calyx lobes than on the calyx tube (Fig. 3d). Corolla white, 5-lobed, tubular-funnelform, with a tube 6.0–8.0 mm long; lobes short, crispate (Wiggins & Porter 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

Distribution and habitat.—Endemic to the Galápagos Islands. This species is found among lava boulders and in rocky soil among other shrubs. It is also sometimes found as an understory shrub in forested areas. *Varronia scouleri* is found from near sea level to 400 m. *Varronia scouleri* on Santa Cruz Island near the Charles Darwin Research Station and town of Puerto Ayora are known to be found among *Bursera graveolens*, *Opuntia echios* var. *gigantea*, *Jasminocereus thouarsii* var. *delicatus*, *Parkinsonia aculeata*, *Croton scouleri* var. *scouleri*, *Waltheria ovata*, *Castela galapageia*, *Cordia lutea*, *Clerodendrum molle*, *Scutia spicata* var. *pauciflora*, *Passiflora foetida*, and *Acacia rorudiana*. Specimens have been collected only from Floreana, Santa Cruz, and Santiago Islands (Fig. 4). This species has the most limited distribution of the endemic Galápagos *Varronia* species.

Specimens examined. **ECUADOR. GALÁPAGOS ISLANDS. Floreana Island:** Dec 1966, Inga Eliasson 836 (S.s.n.); Feb 1928, Borghild Rorud 33 (S.s.n.). **Santa Cruz Island:** Mar 2007, Conley K. McMullen and Michael Shane Woolf 876 (JMUH 13787); Mar 2007, Conley K. McMullen and Michael Shane Woolf 875 (JMUH 13784); Mar 2007, Conley K. McMullen and Michael Shane Woolf 874 (JMUH 13782); Mar 2007, Conley K. McMullen and Michael Shane Woolf 873 (JMUH 13782); Mar 2007, Conley K. McMullen and Michael Shane Woolf 872 (JMUH 13775); Jul 2005, Conley K. McMullen 836 (JMUH 13701); Jul 2005, Conley K. McMullen 835 (JMUH 13697); Jul 2005, Conley K. McMullen 832 (JMUH 13692); Jul 2005, Conley K. McMullen 833 (JMUH 13693); Jul 2005, Conley K. McMullen 834 (13695); Apr 1930, H.K. Svenson 7 (GH 233525); Feb 1967, Ira L. Wiggins and Duncan M. Porter 610 (CAS 528171, GH 244001); Feb 1964, Ira L. Wiggins 18472 (GH 244000); May 1932, John

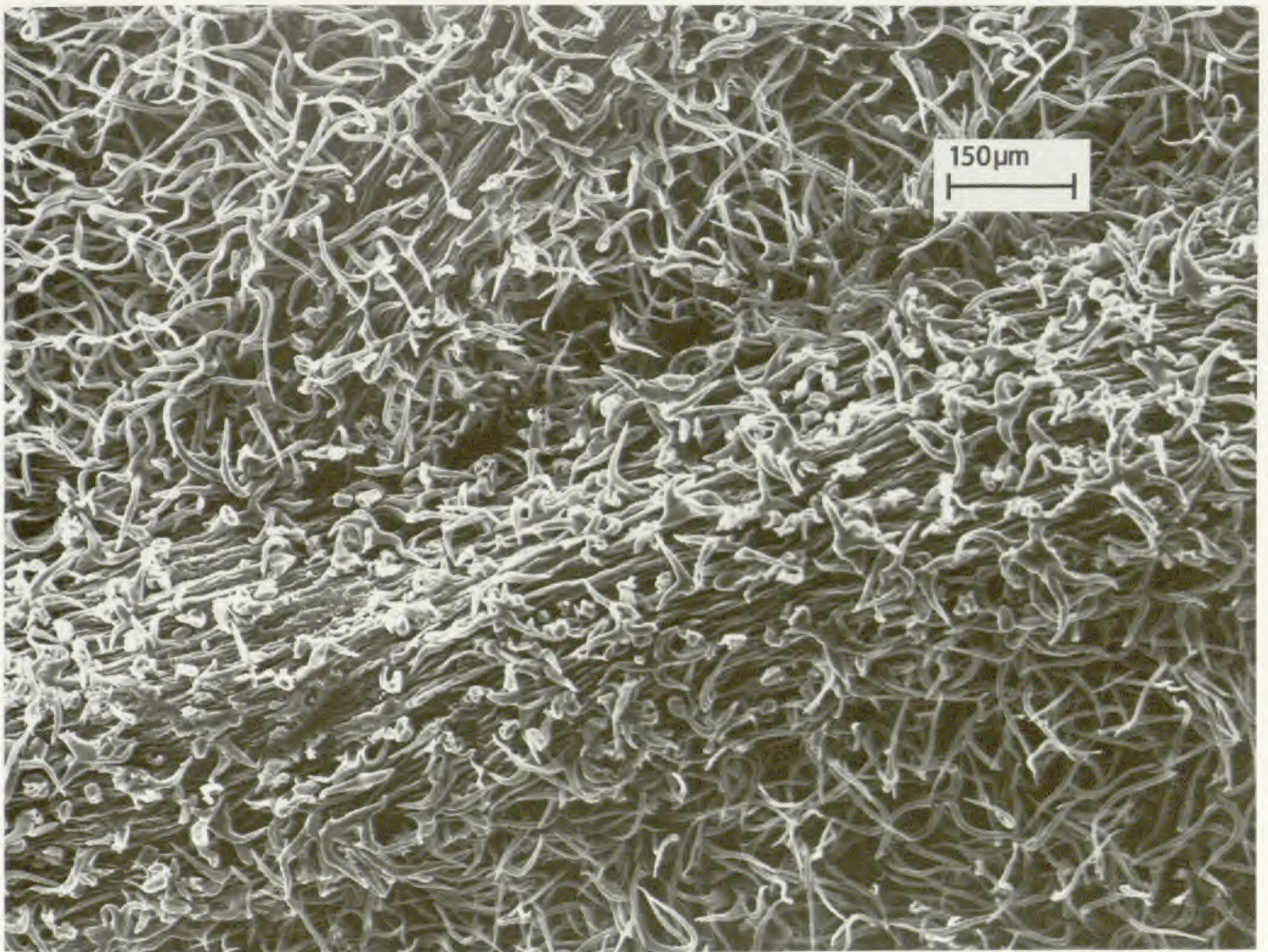


FIG. 14. *Varronia canescens* abaxial leaf surface displaying densely pubescent stellate, simple and forked hairs. Hairs on veins are generally the same size as found in margins. Scale represents 150 μm . Specimen: Jul 2005, Conley K. McMullen, 824 (JMUH 13675).

Thomas Howell 9075 (CAS 468104, GH 233550, NY s.n.); Jan 1964, Syuzo Itow 1 (CAS 579305); Mar 1970, Syuzo Itow 30800-3 (CAS 623522); May 1970, Syuzo Itow 52200-1 (CAS 623519); Feb 1964, Ira L. Wiggins 18472 (CAS 619424); Jun 1970, Syuzo Itow 62600-1 (CAS 623520); Feb 1964, Luis A. Fournier 157 (CAS 705256); Feb 1967, Ira L. Wiggins and Duncan M. Porter 710 (CAS 528135); Feb 1964, Syuzo Itow 45 (CAS 579313); Jun 1932, H.J.F. Schimpff 40 (NY s.n.); 1939, T.W.J. Taylor s.n. (NY s.n.); Jun 1932, H.J.F. Schimpff 40 (BKL 81350, S s.n.); May 1959, Gunnar Harling 5194 (S s.n.); Dec 1966, Inga Eliasson 986 (S s.n.); Jan 1967, Inga Eliasson 1192 (S s.n.); Dec 1966, Inga Eliasson 985 (S s.n.); Dec 1966, Inga Eliasson 990 (S s.n.); Dec 1966, Inga Eliasson 992 (S s.n.); Dec 1966, Inga Eliasson 984 (S s.n.); Jan 1967, Inga Eliasson 1200 (S s.n.); Nov 1966, Inga Eliasson 515 (S s.n.); Nov 1966, Inga Eliasson 513 (S s.n.); Jun 1972, Michelle and Ole Hamann 1598 (C 24/2007/11); Jan 1972, Michelle and Ole Hamann 155 (C 24/2007/9); Jan 1972, Michelle and Ole Hamann 154 (C 24/2007/8); Mar 1981, O. Seberg 1747 (C 24/2007/7); Apr 1972, Michelle and Ole Hamann 1177 (C 24/2007/4); Mar 1972, Michelle and Ole Hamann 726 (C 24/2007/2); Apr 1983, Phyllis S. Bentley 318 (K H2007/01159/12); Apr 1930, H.K. Svenson 7 (K H2007/01159/11). **Santiago Island:** Aug 2005, Conley K. McMullen 864 (JMUH 13758); Aug 2005, Conley K. McMullen 865 (JMUH 13761); Aug 2005, Conley K. McMullen 866 (JMUH 13763); Aug 2005, Conley K. McMullen 867 (JMUH 13764); Aug 2005, Conley K. McMullen 868 (JMUH 13766); Aug 2005, Conley K. McMullen 869 (JMUH 137869); Mar 2007, Conley K. McMullen and Michael Shane Woolf 887 (JMUH 13811); Mar 2007, Conley K. McMullen and Michael Shane Woolf 888 (JMUH 13813); Mar 2007, Conley K. McMullen and Michael Shane Woolf 889 (JMUH 13815); Mar 2007, Conley K. McMullen and Michael Shane Woolf 890 (JMUH 13817); Aug 1891, G. Baur 209 (GH 233524); Aug 1972, Michelle and Ole Hamann 2140 (C 24/2007/3); 1825, John Scouler s.n. (K 449165).

Nomenclatural history.—Hooker first described this species in 1847 as *Cordia scouleri* Hook. f., transferred by Andersson (1855) into *Varronia*, and later *Lithocardium* by Kuntze (1891). Borhidi (1988) renamed the species *Varronia scouleri* (Hook. f.) Borhidi, without regard to Andersson's (1853) designation rendering this combination illegitimate (see Art. 45.3 and Art. 53.1, McNeill et al. 2006). The currently accepted name for this species is *Varronia scouleri* Andersson, based upon Miller and Gottschling's (2007) reinstatement of genus *Varronia*.

Contribution of this study.—Based on characters observed in the type specimen, this species typically has

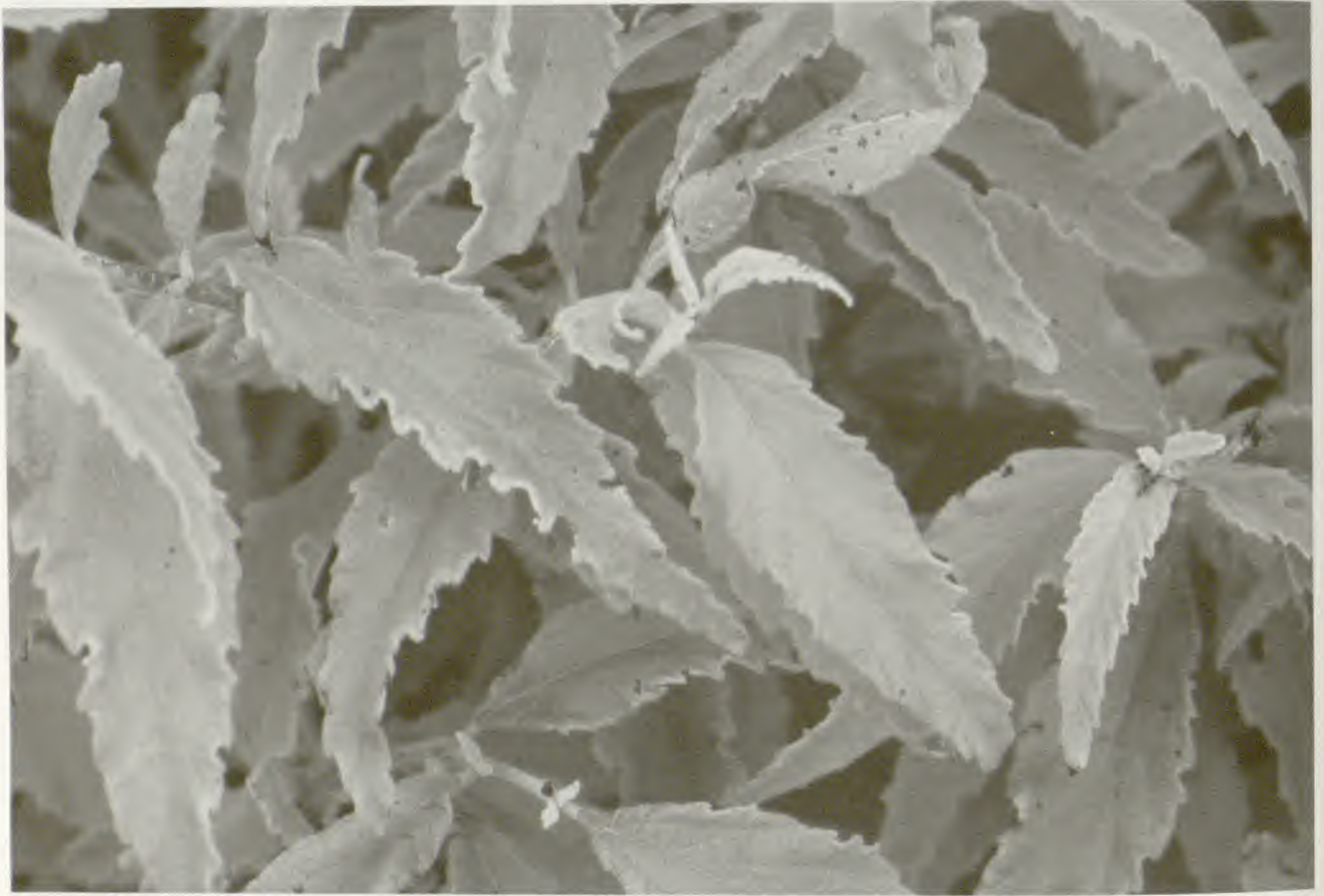


FIG. 15. View of typical *Varronia scouleri* lanceolate leaves with serrate margins. Photograph courtesy of Conley K. McMullen. Specimen: Mar 2007, Conley K. McMullen and Michael Shane Woolf, 889 (JMUH 13815).

lanceolate leaves with coarsely serrate margins (Fig. 15), but this was variable when observing other herbarium specimens. As previously mentioned, *V. scouleri* tends to have longer leaves and more coarsely serrate margins than *V. canescens*, the most similar species. The adaxial leaf surface of *V. scouleri* is pubescent with erect and simple or forked (Fig. 16) or sometimes stellate (Fig. 17) hairs. Abaxial leaf surfaces are sparsely pubescent with appressed stellate and forked, sometimes simple, hairs (Fig. 18). Much longer and more noticeably robust hairs can be found on the veins. These large hairs on the veins are very distinctive of this species. Pubescence of the calyx is composed of erect and simple, and sometimes forked or stellate hairs. Simple hairs on the calyx lobes are noticeably longer than the hairs on the calyx tube. The calyx lobes themselves are usually longer than the calyx tube at anthesis. *Varronia scouleri* is distinct in that its calyx lobes can be exceptionally long and outwardly splayed compared to the other three species.

DISCUSSION

All four species of *Varronia* endemic to the Galápagos Islands deserve recognition as distinct species. Based upon this morphological study, each species can be distinguished by a combination of characters. In addition, these characters appear to have remained constant over the 185 years these species have been collected. While this is not a substantially long period of time in terms of evolution, it does indicate that the characters used in this study remain relatively stable during the time period in which these specimens were collected and studied. No obvious hybrids (plants with characteristics of more than one species) were observed during the morphological study, suggesting that there may be little if any hybridization between species. Based on personal observations, the individual species of *Varronia* do not generally appear to be found within close proximity to one another, further reducing the possibility of hybridization through shared pollinators. Additionally, these *Varronia* species are distylous, and initial research on *V. scouleri* indicates that almost all fruit set is the result of pin

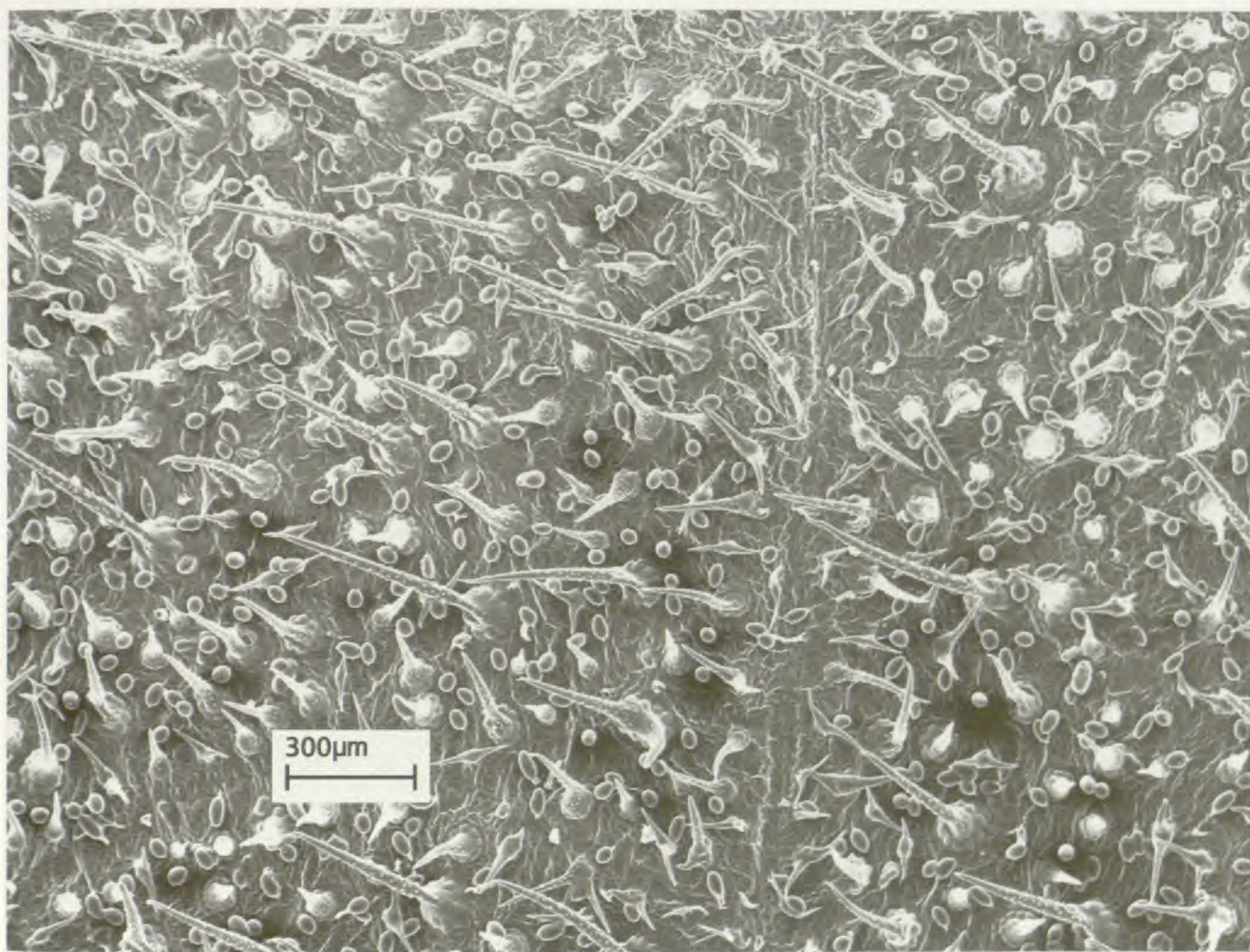


FIG. 16. *Varronia scouleri* adaxial leaf surface displaying erect simple and forked hairs. Scale represents 300 μm . Specimen: Mar 2007, Conley K. McMullen and Michael Shane Woolf, 876 (JMUH 13787).

flowers that have been pollinated with pollen from thrum plants of the same species (CKM and JKS, unpublished data). Thrum plants produce few, if any, fruits, indicating that only about 50% of a local plant population is capable of producing fruit. This initial research also indicates that only about 14% of flowers produce fruits. The limited ability of *Varronia* to effectively produce fruit further limits the possibility of established mature hybrid individuals. Future research on these species will include controlled pollination crosses between species to determine if hybridization is possible, and if so, the viability of the resulting hybrid individuals.

Due to the limited fruiting ability of these species, future recruitment may be cause for concern if the habitat of these species is disturbed. In 1959, the Ecuadorian government created the Galápagos National Park, which comprises about 97% of the total landmass of the archipelago (Camancho 2005). Because such a significant portion of the Islands are part of the National Park, the vast majority of *Varronia* populations are also likely to be in these protected areas. This existing protection decreases the risk of habitat destruction that could potentially reduce the survival of these species. Based on February 2011 observations on Santa Cruz Island near the Charles Darwin Research Station and the town of Puerto Ayora, few seedlings are visible among established populations, though mature adult plants appear to be relatively common and vigorous.

At this time, little is known about the abundance or complete distribution of *Varronia* in the Galápagos, and future field studies of these species would benefit from assessments of these populations. Data from herbarium collection labels has provided enough information to determine on which islands each species can be found (Fig. 4), but specific collection locations were rarely, or only partially provided, apart from those specimens collected by CKM. Based on current information, it is evident that each species retains its foliar morphol-

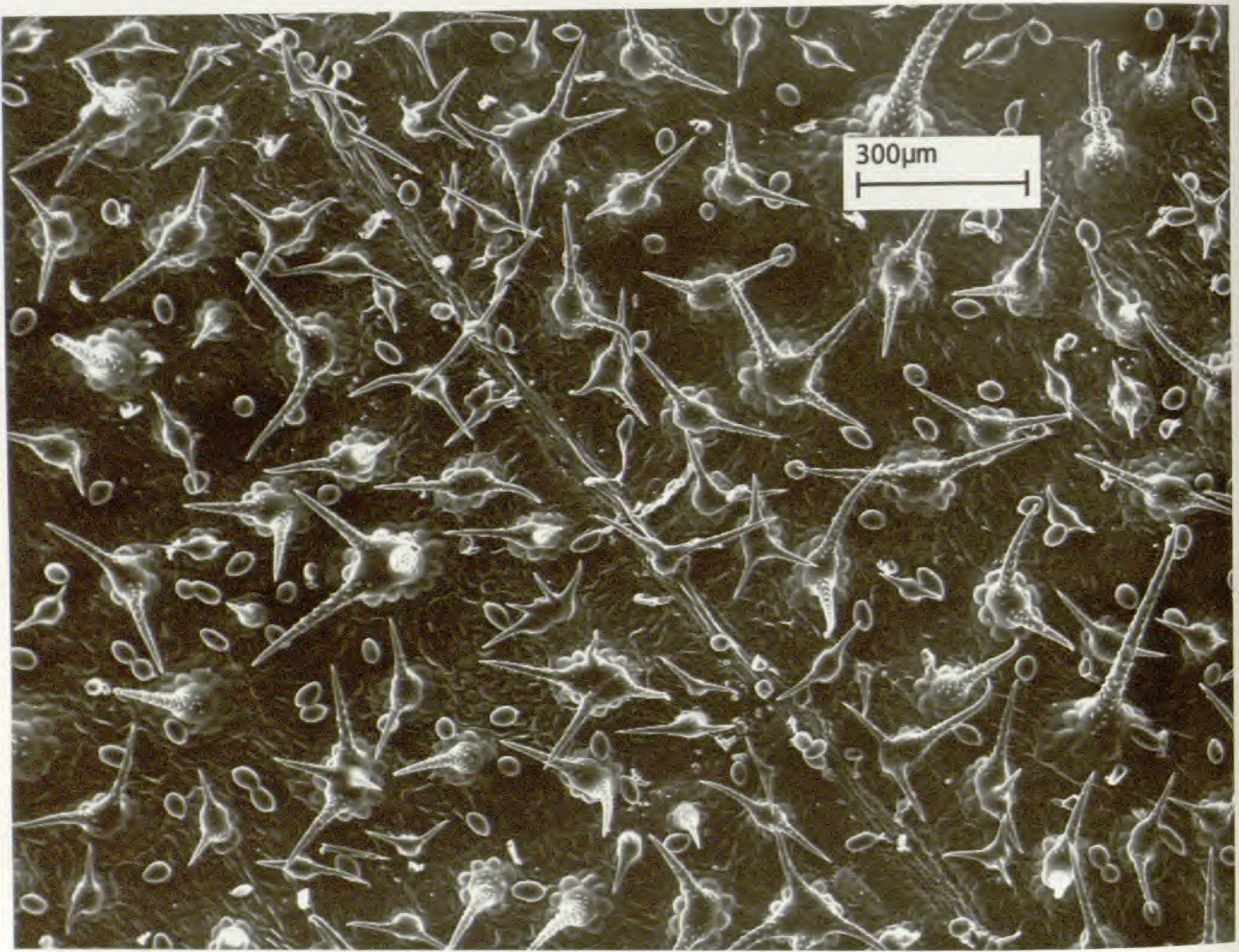


FIG. 17. *Varronia scouleri* adaxial leaf surface displaying erect simple, forked, and stellate hairs. Scale represents 300 μm . Specimen: Mar 2007, Conley K. McMullen and Michael Shane Woolf, 873 (JMUH 13782).

ogy and can be identified across multiple islands suggesting that the characters are not geographically determined. Several islands have all four species of *Varronia* present (Fig. 4). It is possible that this is the result of collection intensity, and future studies may find that the least distributed species may in fact be present on other islands that have not previously undergone intensive collecting. Detailed GPS coordinates for *Varronia* populations in the Islands would provide the information needed to construct more complete distribution maps for each species. These species do not currently appear to be under any increased threat, and their conservation needs are unlikely to change in the near future; however, the IUCN would benefit from updated information and distributions of these species in order to reevaluate, or evaluate for the first time, the status of each species.

This study supports the existence of four morphologically distinct endemic *Varronia* species in the Galapagos Islands. While Weeks et al. (2010), did not find *V. leucophlyctis*, *V. canescens*, and *V. scouleri* to be genetically distinct from one another, this may have been due to the ITS regions that were used in the study. These regions may not be variable if these species have diverged relatively recently. Weeks et al. (2010) suggest that fingerprinting techniques that record nucleotide polymorphisms, such as microsatellites or amplified fragment length polymorphisms, would be a better method for use in the future. Future molecular studies may find that genetic variation exists in now-unexamined regions, but until that time, these populations deserve recognition as morphologically different species based on this study.

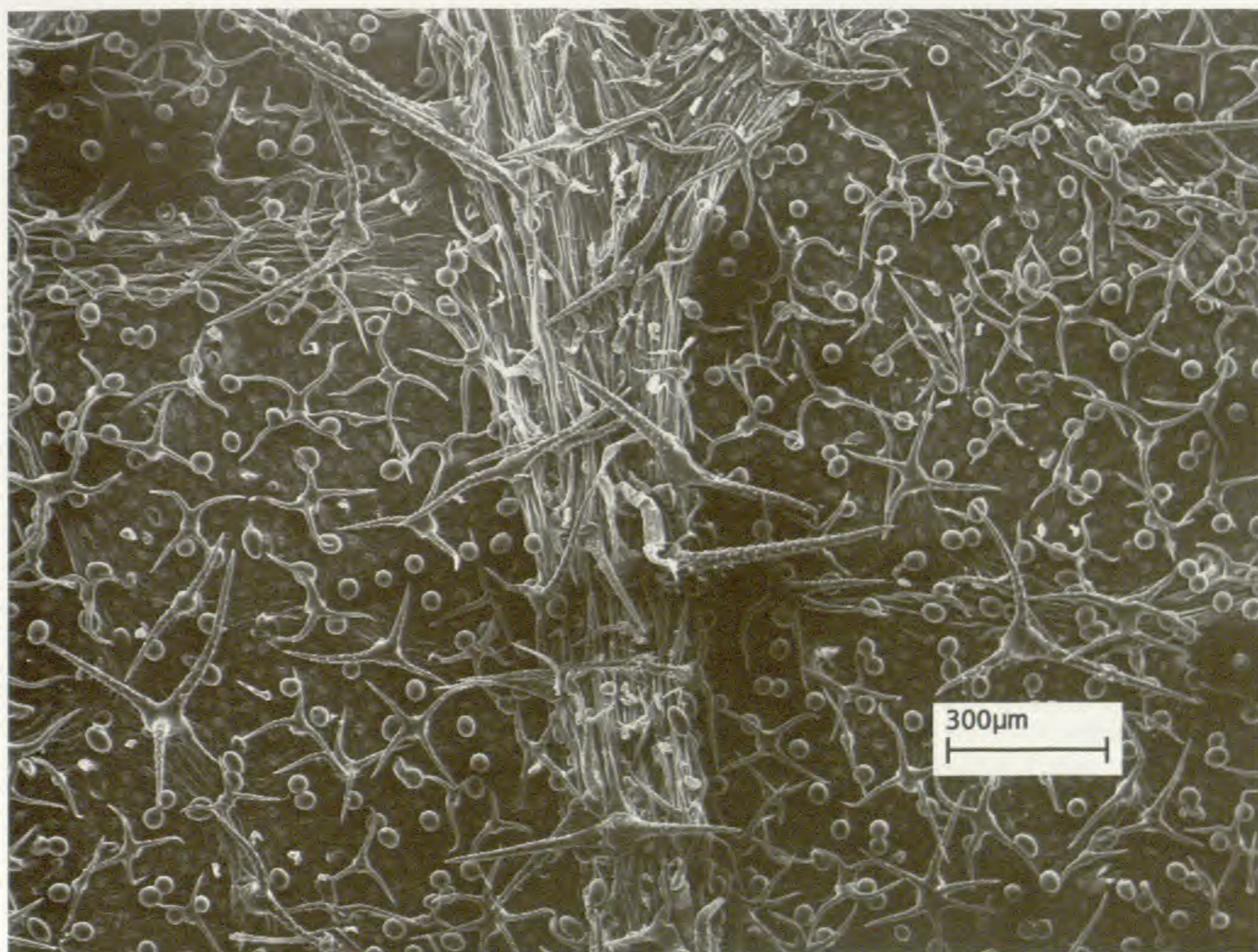


FIG. 18. *Varronia scouleri* abaxial leaf surface displaying robust simple, forked and stellate hairs on veins, and smaller, appressed stellate hairs in margins. Scale represents 300 μm . Specimen: Mar 2007, Conley K. McMullen and Michael Shane Woolf, 873 (JMUH 13782).

CONCLUSIONS

Morphological characterization indicates the existence of four endemic species of *Varronia* in the Galápagos Islands that are distinct. The results from this study will be helpful in evaluating these species for their conservation statuses. Over 100 misidentified specimens are now correctly identified through the course of this study, and the diagnostic information provided here in the new taxonomic keys will help provide the information necessary for other specimens to be reevaluated, or new collections to be correctly identified. In addition, an effort must be made to assess the size and stability of the populations of each endemic *Varronia* species in order to evaluate how these species should be managed. Protecting the endemic species of the Galápagos is important both for the survival of the individual species as well as the continuation of the Galápagos Islands as a unique example of island evolution and diversity. Effective conservation programs to protect this exceptional diversity can only result from research that strives to document the flora and fauna of these islands. Accurate descriptions of the distinctive species of the Galápagos, such as those accomplished in this study, are the first step towards protecting and ensuring their future on the islands.

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